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On the Oxygen Consumption of Ancyliidae (Gastropoda) from an Ecological Point of View.

By KAJ BERG

(Freshwater-biological Laboratory, University of Copenhagen.)

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1. INTRODUCTION

It is a well known fact that the two related snails, *Ancylus* (= *Ancylastrum*) *fluviatilis* (O. F. Müller) and *Acroloxus* (= *Ancylus*) *lacustris* (Linné) are found in heterogeneous environments; the former occurs mainly in running water, it is rheophilous. It lives in springs as well as in brooks and rivers. It is nearly always found

on a stony bottom, sometimes in a swift current. It may also occur, but rarely, on the shores of some lakes (see e.g. GEYER, 1927, p. 151). As a substratum it prefers smooth stones covered with a thin layer of diatoms and other algae. The latter, *Ac. lacustris*, is found in stagnant water — it is limnophilous. It is especially seen on stems of big aquatic plants, particularly on those overgrown with a slimy layer of algae. If it appears in water-courses it is chiefly in the reed-swamp, in which the current is hardly perceptible. Although it prefers environments with still water, it is possible for it to exist in places in which there is a very slow current.

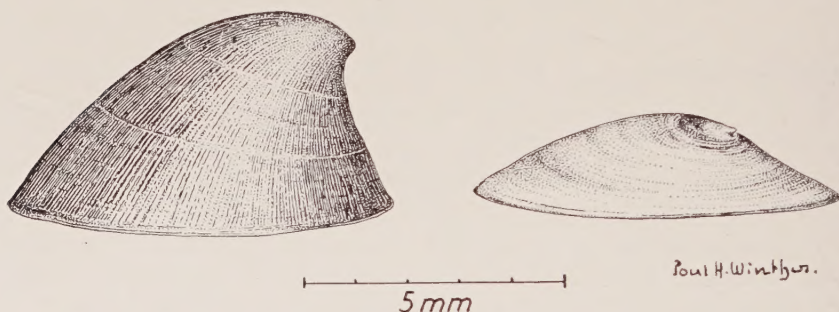


Fig. 1. *Ancyclus fluviatilis* (left) and *Acroloxus lacustris* (right).

About both species it can be said that they have a wide distribution, and that they occur in great numbers in suitable localities; on the distribution and other details of their occurrence in this country see e.g. BERG, 1948, p. 194 ff. and KAISER 1950, p. 69.

Since *Ancyclus fluviatilis* prefers running water with more or less current, while *Acroloxus lacustris* prefers stagnant water, the question arises as to the causes of this characteristic distribution. Obviously the external shape of the species (fig. 1) is of no importance in the distribution. In spite of the fact that *An. fluviatilis* has the highest shell, which must be supposed to offer the greatest resistance to the current, it is found in running water. *Ac. lacustris*, however, the shell of which is very low and which cannot therefore offer much resistance to the pressure of a possible current, mainly lives in stagnant water.

The explanation of the distribution of the two species might perhaps be found elsewhere, viz. in differences in their respiratory requirements. Has the rheophilous *An. fluviatilis* a greater oxygen consumption than the limnophilous *Ac. lacustris*? Is the oxygen consumption of *An. fluviatilis* more easily affected by alterations in the oxygen content of the water than that of *Ac. lacustris*? Is the

oxygen consumption of *An. fluviatilis* at high temperatures stopped irreversibly sooner than that of *Ac. lacustris*? It is reasonable to ask this last question, for in localities inhabited by *An. fluviatilis* the temperature of the running water must be supposed to attain summer maxima which are often somewhat lower than in the stagnant water environment of *Ac. lacustris*.

While the investigation of these questions has been in progress similar ideas have been entertained in other quarters. In his discussion of the occurrence of *An. fluviatilis* in the big post-glacial lake, the *Ancylus*-lake, TORSTEN GISLÉN, (1945) advances the opinion that the species requires well-circulated water, abounding in oxygen. And NILS HJ. ODNER (1941, p. 15) writes that *Ac. lacustris* is almost insensitive to oxygen lack and in addition can live several days in water which has been depleted of oxygen by boiling. *An. fluviatilis*, which requires more fresh water, can often be seen to have climbed up above the surface of the water in aquaria, obviously because of its need of oxygen. But the correctness of these views has not hitherto been examined by means of respiration experiments.

Some examples of low oxygen saturation of the water in *Ac. lacustris* localities may be stated: *Karl's Lake*, March 6th, water temperature 0.3°C , thickness of ice 22 cm: 23 % of oxygen saturation. The *River Suså*, outflow in Tystrup Lake, still water, July 25th, water temperature 23.9°C : 76 % of oxygen saturation. The same locality, July 29th, temp. 17.0°C : 87 % of oxygen saturation; Aug. 23th, temp. 17.2°C : 84%; Aug. 25th, temp. 18.0°C : 77 %; Aug. 26th, temp. 19.5°C : 57 %. *Törkeri Lake*, Oct. 1st, temp. 10.4°C : 73 %. *Karl's Lake*, Nov. 13th, temp. 5.0°C : 83 %. *Törkeri Lake*, Nov. 13th, temp. 5.5°C : 24.2 % of oxygen saturation.

In cavities below withered leaves, on stems of plants, where *Ac. lacustris* lives, the oxygen concentration may perhaps be still lower.

Prior to and simultaneously with this investigation H. MUNRO FOX and his collaborators (B. G. SIMMONDS, R. WASHBOURN, C. A. WINGFIELD and B. M. WALSHE) have carried out valuable investigations on the oxygen requirements of many arthropods from running water and stagnant water. Thus WALSHE (1948) has shown that "two Chironomid species from a stream have higher metabolism rates in aerated water than the corresponding species from still water". An important result of the work of MUNRO FOX and his collaborators in this field has been formulated by WALSHE (p. 40) as follows: "The fact that relatively high metabolic rates have also been found in stream species of other aquatic arthropods (Fox et al. 1933, 1935) suggests that *this property may be a general characteristic of animals living in streams.*"

It will appear below whether this general rule also applies to the two molluscs here examined. The object of the following experiments is to find out the oxygen consumption under different con-

ditions in order to gain some idea of the actual requirements of the two species in nature.

I am indebted to Mr. AXEL M. HEMMINGSEN, Ph. D. for valuable advice concerning this investigation and I thank him very much for the help given. I also wish to express my cordial thanks to Mr. KAY BRUNFELDT, M. Sc. who several times assisted me in technical questions relating to the oxygen determination. He also carried out some experiments for the purpose of verifying my results by means of an apparatus constructed by himself. I very much appreciate his valuable assistance. I acknowledge with gratitude a grant from the CARLSBERG FOUNDATION in support of my work. My sincere thanks are also due to Dr. B. M. WALSH and Miss BARBARA GILCHRIST, both of whom read the manuscript and corrected the English; and to Mr. H. F. STENBY, C. E., who made some calculations.

2. METHODS

The oxygen determinations were made according to the WINKLER method (1914, p. 665), as developed in the Zoophysiological Laboratory, University of Copenhagen. A microburette was used for the titration and syringe pipettes for withdrawing the water samples. After the two WINKLER reagents have been added the chemical reactions occur inside the syringes and the same is the case with the dissolution of the deposit after the admixture of HCl (KROGH 1935, p. 135).

In most cases 20 individuals of *An. fluviatilis* or 100 individuals of *Ac. lacustris* were used for each experiment because of the different size of the species. In each experiment the animals of each species were almost the same size. By the use of a great number of individuals it was attempted to avoid the influence of an individual variation and at the same time to obtain an oxygen consumption great enough to be measured by the procedure employed.

The animals were caught in nature and — unless otherwise stated — brought to the laboratory and at once used for experiments. As a rule the experiments could be started about 1 hour after the collection had been completed. None of the animals had therefore been long in the aquarium of the laboratory before the start. Narcotics were not used. The animals were placed in a bottle, the capacity of which was measured exactly. From a container holding several litres, water with the desired oxygen was washed through the bottle. The oxygen content was determined. The bottle containing the animals was closed with a glass stopper, wrapped up in black paper, and placed in a water bath at the desired temperature. (If the tempe-

perature of the water-bath sometimes differed a little from the desired temperature, the results were corrected for this temperature deviation by means of the correlation found between the oxygen consumption and the temperature.)

Experiments in which the bottle was not wrapped up in black paper turned out to be quite worthless, for in light the layer of algae on the shells of the snails can at times produce as much oxygen as the snails consume. Before the experiments the shells of the snails covered with algae were brushed, so the main part of the algae was removed.

After the experiment had been in progress for some time — unless otherwise stated, 1 hour — the bottle was taken out of the water-bath, shaken, and the oxygen content was again determined. The difference of the oxygen content of the water before and after the experiment was due to the respiration of the animals. In part 3 experiments of longer duration are described. Each oxygen determination was carried out as an average of 2 (or 3) single determinations. The single determination was accurate to the extent that the maximum variation around the average of a series of determinations of the same oxygen-saturated water at room-temperature was ± 0.04 ml O_2/l ; the standard deviation under these conditions was ± 0.022 ml O_2/l .

After each experiment the animals were dried on filter-paper and weighed, then killed. The shells were removed and weighed in the dry state. The difference between the first weighing and the weight of the shell is the weight of the soft tissues of the animals (live weight). The oxygen consumption of the animals was calculated in relation to this weight.

In the dark, during the experiment, the animals hardly moved. After the experiment most of the animals were lying or sitting on the bottom of the bottle as before the experiment started. Some, however, had climbed a little way up the sides of the bottle, but rarely more than half-way. In nature these animals do not move very much either. During the experiments the animals do not eat, except perhaps when some of them eat a little of the algae from the shells of the other snails.

The above-mentioned experimental conditions cannot be called standard conditions (see e.g. KROGH 1916, p. 57 and 1941, p. 7), but still I think they are an acceptable approximation to such. Standard conditions demand that voluntary muscular movements of the animals are eliminated and no food is being digested or absorbed. As already mentioned, the movements of the Ancyliidae in the dark respiration bottle are very small or lacking. During the experiments no food, or very little, is eaten, but food eaten before the experi-

ments is perhaps digested or absorbed to some degree. This, however, hardly influences the results perceptibly, since a short period of starvation before the experiments does not seem to diminish the oxygen consumption (p. 233).

As is well known, in warm-blooded animals complete rest in a starving condition is characterized by a definite level of metabolism, the so-called standard or basal metabolism. But "it is important to note that in many cold-blooded animals there is no such well-defined basal level" (KROGH 1941, p. 7, cp. ZEUTHEN 1947, p. 45); during adverse conditions the metabolism keeps on decreasing until death supervenes. Since the present experiments were carried out shortly after catching the animals (unless otherwise stated), and since the sluggish animals were obviously resting or nearly so, and their food digestion and absorption presumably was almost as in nature, I think that the figures obtained must be nearly valid for natural conditions.

3. OXYGEN CONSUMPTION WITH INCREASING DURATION OF THE EXPERIMENTS AND WITH DECREASING OXYGEN CONTENT.

It was the purpose of these experiments to find out whether *An. fluviatilis* and *Ac. lacustris* can maintain a constant oxygen consumption when the experimental period is gradually prolonged and the oxygen content of the water, at the end of the experiment, grows less and less.

Notes on the experiments. The *An. fluviatilis* which were used for the experiments, were collected in Eskildstrup Møllebæk (mill-brook), near Sorø, in August. 20 adult animals of about the same weight were placed in each bottle of about 70 ml for respiration. The bottles were filled with water from the brook at a temperature of about 16° C. This water receives a contribution of spring- and subsoil water and consequently was not quite saturated with oxygen. In August its temperature varied from about 13° C to about 20° C under the influence of the water supply from the mill-pond. The experiments were started in nature immediately after the collection, the respiration bottles being placed in a water-bath (thermostat), at about 16° C, which was then carried to the laboratory (2 km). A series of 11 experiments was made, lasting respectively $\frac{1}{2}$, $1\frac{1}{4}$, 2, 3, 5, 6, 7, 7, 8, 9 and 11 hours.

The specimens of *Ac. lacustris* were collected in August in stagnant water in the reed-swamp at the entrance of the river Susaa into

Tystrup lake. The water of the locality was not quite saturated with oxygen. Its temperature was about 19° C. In nature, immediately after the collection, about 100 adult individuals of about the same weight were placed in each respiration bottle of about 70 ml. The bottles contained spring-water almost saturated with oxygen. The experiments were carried out in exactly the same way as the above-mentioned. In this case two series of experiments were made, the first one comprising 10 experiments of a duration of $\frac{1}{2}$, $1\frac{1}{4}$, 2, 3, 5, 6, 7, 7, 8 and 10 hours respectively, the second one including 6 experiments lasting $\frac{1}{2}$, $1\frac{1}{4}$, 2, 3, 5 and 6 hours.

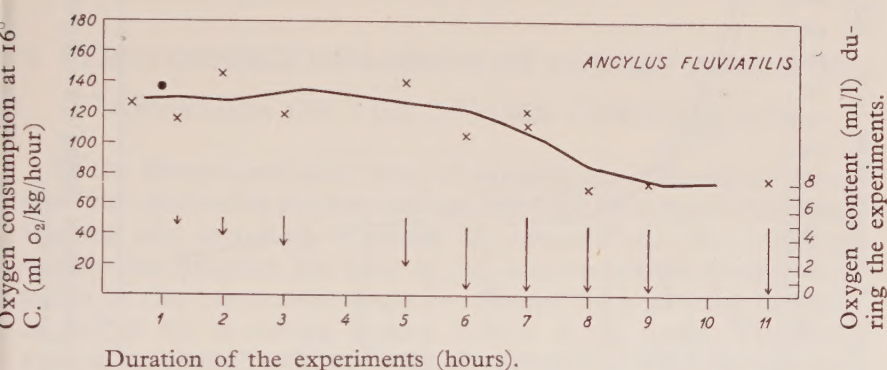


Fig. 2. *Ancylus fluviatilis*. The curve indicates the oxygen consumption in experiments of varying duration. The size of the arrows indicates the decline of oxygen concentration during these experiments. As to the filled circle see the text p. 234.

The result of these series of experiments is indicated in figs. 2 and 3. In fig. 3 the continuous curve shows the first series of experiments on *Ac. lacustris*, the dot-and-dash line shows the second series. The oxygen consumption has been plotted along the ordinate, the duration of the experiment along the abscissa. The length of the arrows under each result indicates the decrease in the oxygen content during the experiment concerned (see right ordinate). In fig. 3 the brackets along the arrows show the decrease of the oxygen content in the experiments of the second series.

Fig. 2 shows that *An. fluviatilis* has a stable oxygen consumption of 120—140 ml/kg/hour at 16° C in experiments the duration of which varied from $\frac{1}{2}$ —5 hours, and the final oxygen content of which varied from 5—2 ml/litre. In experiments of a duration of 6 or 7 hours and with a further decrease in the final oxygen content the oxygen consumption of the species seems only to be slightly diminished. But in the experiments lasting 8, 9 and 11 hours the animals showed a

distinct decrease in the oxygen consumption per hour; the oxygen is then finally almost spent.

The behaviour of *Ac. lacustris* is quite different. It has an unstable oxygen consumption (fig. 3). In the first experiment lasting only $\frac{1}{2}$ hour and with a small oxygen decrease from about 6.8 to about 5.8 ml/litre a great oxygen consumption was found, 285 ml/kg/hour

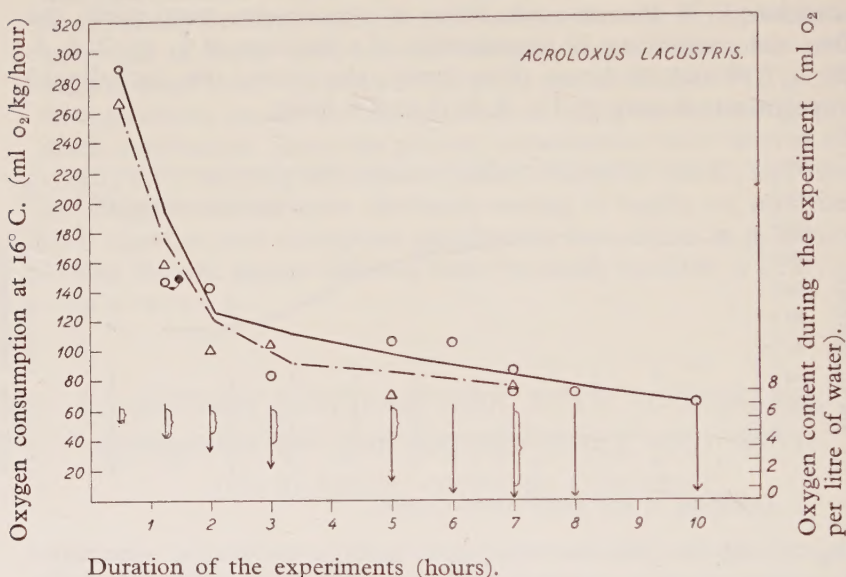


Fig. 3. *Acroloxus lacustris*. The upper curve indicates the oxygen consumption in a series of experiments of varying duration (circles). The decline of oxygen concentration in these experiments is indicated by the arrows below. The dot-and-dash line indicates the oxygen consumption in another series of experiments (triangles) carried out in the same way as the first. The declines of oxygen concentrations during the lastnamed series are somewhat less than in the first series and indicated by the brackets along the arrows. As to the filled circle see the text p. 234.

(upper curve). But already in the second experiment, which lasted $1\frac{1}{2}$ hours, the oxygen consumption per hour decreased to half the value, in spite of the fact that at the end of the experiment the oxygen content of the water of the respiration bottle was more than 66%. The decline in the oxygen consumption per hour was continued, but less abruptly with increasing duration and a decreasing final quantity of oxygen. Thus on the whole the curve showing the oxygen consumption of *Ac. lacustris* has a different form from that showing the oxygen consumption of *An. fluviatilis*. The second series of experiments — the dot-and-dash curve fig. 3 — confirms the information of the first series.

(The results of the experiments of a duration of $\frac{1}{2}$ hour are in this case a little greater than found in similar experiments later on, possibly because the animals in the present experiments moved somewhat more than usually).

The result that the species from running water, *An. fluviatilis*, has a stable respiration, and that the species from stagnant water, *Ac. lacustris*, has an unstable respiration under these conditions was the opposite of what might have been expected.

The correlation between the oxygen concentration of the environment and the oxygen consumption of the two species will be illustrated by the experiments described in part 5.

4. THE POSSIBLE INFLUENCE OF A SHORT PERIOD OF STARVATION ON THE OXYGEN CONSUMPTION.

In the above-mentioned series of experiments of increased duration with decreasing oxygen content, the time the animals had been starving also increased. It might be supposed that the declining oxygen consumption per hour of *Ac. lacustris* with increasing duration of the experiment might be affected by a growing hunger, as well as by decreasing oxygen content in the water. Therefore experiments were performed with *Ac. lacustris* in which the animals had been starved for some hours before the experiments. For comparison a quite similar experiment was made with *An. fluviatilis*.

For this experiment 125 individuals of *Ac. lacustris* were collected in the reed-swamp at the entrance of the river Susaa into Tystrup Lake, and put into a cage, which was lowered into the water in this reed-swamp. The animals were adults and about the same weight as in the previous experiments. The experiment took place in July. The temperature of the water was about 24°C , the air saturation was about 77%. So the animals were living in their usual environment, but they were unable to consume their usual food, the layers of algae on the rushes. Some of the animals may possibly consume some food from the algal layers on the shells of other animals. The starvation period lasted $5\frac{1}{2}$ hours. Then the animals were removed from the cage and immediately submitted to a respiration experiment lasting $1\frac{1}{4}$ hours (On experiments of about this duration cp. p. 237).

In a similar way 21 individuals of *An. fluviatilis* were collected in Eskildstrup Møllebæk, Sorø, and placed in a cage in the brook, so that the water of the brook could wash freely round the animals. Consequently they were also unable to get any food in the normal way. After $5\frac{1}{2}$ hours they were taken out of the cage and submitted to a respiration experiment of a duration of 1 hour. This experiment,

too, was carried out in July; the temperature of the brook-water was 16.7°C and its oxygen saturation about 78%.

The results of the two experiments with animals that had been starved is indicated by a filled circle in figs. 2 and 3. (In the last case the circle could not be drawn with the correct abscissa owing to lack of space. It should be moved a little to the left, as shown by the arrow). It is seen that the oxygen consumption of *An. fluviatilis* had not diminished in spite of the starvation period of $5\frac{1}{2}$ hours before the experiment; this agrees very well with the fact that *An. fluviatilis* can be subjected to experiments for 5 hours — that is, starved for 5 hours — without any decline in the oxygen consumption, as indicated by the curve in this figure.

It is also seen that the quantity of the oxygen consumed by *Ac. lacustris* is in no way influenced by the starvation period of $5\frac{1}{2}$ hours before the experiments. Consequently the declining oxygen consumption found in this species with increasing duration of the experiments is not due to hunger — at any rate not in experiments of a duration of $5\frac{1}{2}$ hours + $1\frac{1}{4}$ hours — but must be due to the decline of the oxygen content occurring at the same time.

Nor does the oxygen consumption of *Ac. lacustris* collected in winter seem to be diminished by a brief period of starvation: in January about 300 *Ac. lacustris* individuals of about the same size (on the average 7.54 mg) were brought to the laboratory in Hillerød from Esrom Lake, the temperature of which was about 3°C . Half of them were kept in a frigidaire at about 5°C in a flat dish of water but without food. The rest of the animals were immediately submitted to a respiration experiment lasting 1 hour (cp. p. 237) in the usual way. The result was that these animals used 108 ml/kg/hour at 16°C . The animals placed in the frigidaire after 4 hours, too, were submitted to a respiration experiment of 1 hour. The result of this experiment was an oxygen consumption of 121 ml/kg/hour. The latter animals having thus starved for 4 hours longer than the former, nevertheless did not have a smaller oxygen consumption. But perhaps in nature at such low temperatures the animals had not consumed any food for rather a long time; in which case it is understandable that the starvation period of 4 hours prior to the experiments is of no importance.

5. THE OXYGEN CONSUMPTION AT VARIOUS OXYGEN CONCENTRATIONS OF THE WATER.

The running water in which *An. fluviatilis* lives, generally has an abundant oxygen content, unless the water-course is polluted, or it

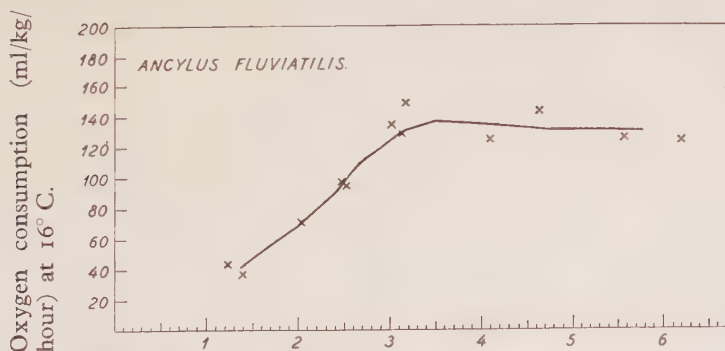
receives large contributions of spring-water deficient in oxygen (subsoil-water).

In stagnant water, the habitat of *Ac. lacustris*, — e.g. the water in a dense reed-swamp (cp. BERG 1943, p. 138) — it must be supposed that at times the oxygen content declines considerably below saturation. Therefore it is of interest to see how the respiration of the 2 species behaves in water with differing oxygen contents.

Notes on the experiments. Water saturated with N_2 was mixed in different proportions with water aerated with atmospheric air. In this way water of the various oxygen concentrations desired was produced. The respiration bottle, the capacity of which was about 70 ml, was washed with water of the desired oxygen concentration before an experiment, but after the animals had been placed in it. The oxygen concentration was measured. After 1 hour the oxygen content of the respiration bottle was measured. The difference constitutes the oxygen consumption. In the experiment with *An. fluviatilis* the decline of the oxygen concentration during the experiment was 0.25—0.79 ml/litre. In the experiments with *Ac. lacustris* there was a similar decline, except in experiments in saturated or almost saturated water, in which it was 1.17 and 1.08 ml/litre.

An. fluviatilis was collected in Eskildstrup Møllebæk, Sorø, *Ac. lacustris* mainly in Törkeris Lake near Hillerød. The animals were transported to the laboratory in Suserup, near Sorø, and to the laboratory in Hillerød respectively, and the respiration experiments were started about 1 hour after the collection was completed. During the transport to the laboratory, *Ac. lacustris* was on *Scirpus lacuster*, overgrown with diatoms, as is the case in nature.

The result of the two series of experiments is seen in figs. 4 and 5. The oxygen consumption at 16° C is plotted along the ordi-



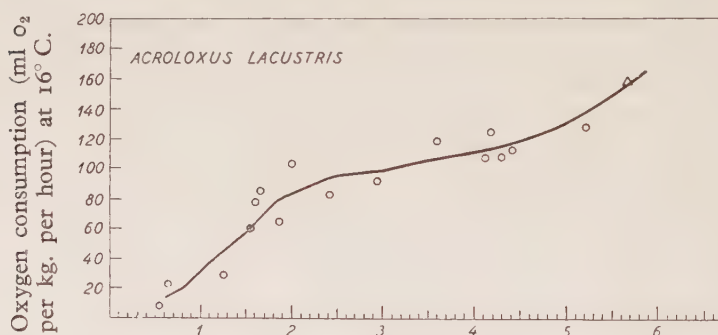
Average oxygen content during the experiments (ml O_2 per litre of water).

Fig. 4. *Ancylus fluviatilis*. Oxygen consumption in relation to the oxygen content of the water.

nate, and the average oxygen concentration during the experiments along the abscissa. From the curve in fig. 4 it appears that *An. fluviatilis* maintains an oxygen consumption of about 130—140 ml/kg/hour, even if the average oxygen content is changed from about 6 to about 3 ml/litre. But if the average oxygen content falls below 3 ml/litre there is a great decrease in the oxygen consumption. The curve shows a distinct bend.

The fact that *An. fluviatilis*, as just seen, has a stable respiration even if the oxygen content of the water falls far below saturation, agrees very well with the result found above (cp. p. 231).

In considering these experiments it must be remembered that the respiration takes place in a closed respiration bottle with stagnant water. Thus it is possible that the animals on the bottom of the respiration bottle were surrounded by a lower oxygen content of the water, than stated by the average oxygen content.



Average oxygen content during the experiments (ml O₂ per litre of water).

Fig. 5. *Acroloxus lacustris*. Oxygen consumption in relation to oxygen content of the water (duration of every experiment 1 hour, cp. p. 237) The triangle indicates the mean value of ten earlier experiments.

The curve of *Ac. lacustris* (fig. 5) takes a different course from that of *An. fluviatilis*. As soon as the oxygen content of the water sinks below the average 6 ml/litre the oxygen consumption of *Ac. lacustris* sinks too; it continues to decline with the decreasing oxygen content of the water. The oxygen consumption of *Ac. lacustris* at 16° C is thus unstable: the species is unable to maintain its normal oxygen consumption at an oxygen content decreasing to 3 ml/litre, as *An. fluviatilis* can.

The result of the experiment, that *Ac. lacustris* has an unstable respiration as soon as the oxygen content declines somewhat below saturation, agrees very well with the experiments mentioned on page 232.

As already stated, the curve for *Ac. lacustris* is based on experiments which were started in the laboratory about 1 hour after the collection of the animals. The experiments lasted 1 hour. The oxygen consumption found in this way cannot be expected to attain such high values — according to fig. 3 — as the oxygen consumption in brief experiments (of a $\frac{1}{2}$ hour's duration) having a smaller oxygen decline. Therefore the oxygen consumption just found cannot be used in direct comparison with the oxygen consumption of other species e.g. *An. fluviatilis*.

6. OXYGEN CONSUMPTION AT VARYING TEMPERATURES.

Many water-courses — springs and brooks — in which *An. fluviatilis* live, have a low summer-temperature, whereas the summer-temperatures of habitats in rivers are higher. Nevertheless it must be supposed that the latter temperatures cannot be quite as high as the summer-temperature of the shallow, still water, to which *Ac. lacustris* belongs. At the outset it would be reasonable to expect that *An. fluviatilis* was adapted to somewhat lower temperatures than *Ac. lacustris* and that it cannot endure such high temperatures as the latter. Therefore two series of experiments were carried out, in which the oxygen consumption of the two species at temperatures varying from about 3—6° C and 36—40° C was examined. The variation of the oxygen consumption of *An. fluviatilis* with the temperatures was ascertained both for big individuals weighing ca. 20—30 mg (the live tissues) and for small individuals of about 5—7 mg. The weight of the *Ac. lacustris* individuals was about 5—6.5 mg (the live tissues). The results have not been corrected for differences in the average weights between the individual experiments.

The animals for the experiments with *An. fluviatilis* were mainly caught in Eskildstrup Møllebæk, near Sorø. The experiments were carried out in August. During the day the temperature of the brook was mostly about 16° C and the air saturation about 80⁰„. For the experiments with *Ac. lacustris*, animals were used from the still water of the reed-swamp of the river Susaa near its entrance into Tystrup lake and from Esrom Lake. The experiments were carried out in September. In the daytime the temperature of the river was mostly about 15° C and the air saturation about 80⁰„. The temperature of Esrom Lake was about 14—18° C and at that time of the year the surface water is saturated with air. After the animals had been caught they were carried to the laboratory. During the transport *Ac.*

lacustris was attached to *Scirpus lacuster*. After the return the animals were immediately subjected to experiments. For *Ac. lacustris* the duration of these experiments was 1 hour, for *An. fluviatilis* usually the same.

The result is seen in figs. 6 and 7 in which the temperature of the experiment is plotted along the abscissa in the usual way, and the oxygen consumption along the ordinate in a logarithmic scale. In such a coordinate system the relation between the oxygen consump-

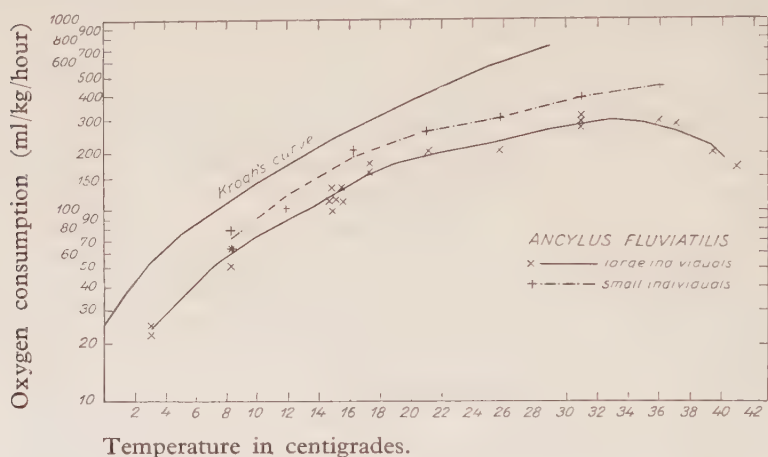


Fig. 6. Rate of oxygen consumption of *Ancylus fluviatilis* in relation to temperature. Above is drawn a Krogh's curve (1914, p. 504) for comparison, the curve being made in this case in a logarithmic scale along the ordinate.

tion and the temperature would appear as a straight line if the oxygen consumption increased by the same percentage over the whole temperature-range investigated. Thus deviations from such a relation appear clearly. For the description of the oxygen consumption in a logarithmic scale see p. 241.

The oxygen consumption of big individuals of *An. fluviatilis* increases from about 25 ml/kg/hour at 3° C to almost 300 ml/kg/hour between 31 and 36° C. This temperature interval is the maximum the big individuals can endure — at any rate for a short time — before the respiratory system is destroyed. If the temperature increases further, the oxygen consumption decreases abruptly. At 36°—40° death may occur during the experiments.

The maximum summer-temperature which we have been able to find — from this laboratory — in a water-course, in which *An. fluviatilis* was prevalent, is 25° C (P. M. JÓNASSON p. 209 in BERG 1948). As the species also lives in springs, in which the maximum summer-temperature in the localities is mostly about 10° C — e.g.

in Ravnkilde in Himmerland (North Jutland) according to kind information from Mr. ANKER NIELSEN, Ph. D. — it is unexpected to find that at such high temperatures as 31° — 36° C it has an oxygen consumption indicating that the animals are not yet hurt by the high temperatures.

The oxygen consumption of *Ac. lacustris* in experiments lasting 1 hour (cp. p. 237) increases from about 50 ml/kg/hour at 6° C to about 330 ml kg hour at 31° C, after which it declines abruptly. At 35° — 36° C many animals die during the experiments. As seen from the results, the maximum temperature which *Ac. lacustris* can endure before the respiration is disturbed is not higher than in the case of *An. fluviatilis*. In the experiments at about 31° C some of the animals already die.

As is well-known, KROGH (1914, p. 504) developed a curve on the quantitative relation between the temperature and the standard metabolic rate in animals. By the standard metabolic rate he means the metabolism when conditions involve a minimum activity of the animal and no food is being digested. In fig. 6 KROGH's curve is shown; its ordinates are here plotted on a logarithmic scale, an arbitrary starting point being chosen. KROGH's curve shows that with increasing temperature the oxygen consumption increases, but with a percentage decrease.

Fig. 6 shows that below about 18° C the increase in the oxygen consumption of *An. fluviatilis* with increasing temperature is the same as according to KROGH's curve, but at higher temperatures than about 18° C the increase is smaller. The diminished increase of the

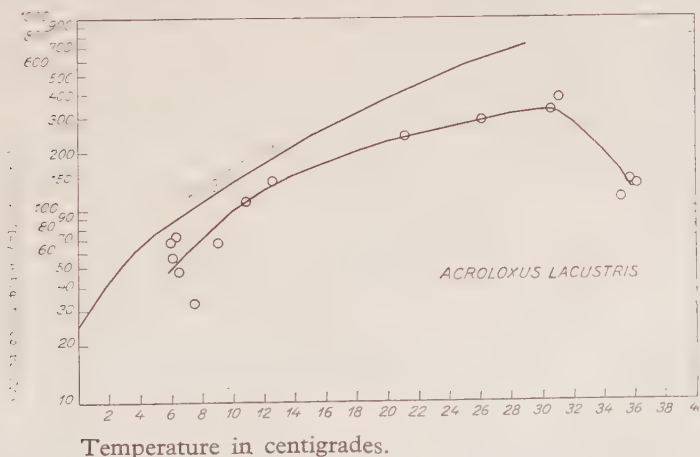


Fig. 7. Rate of oxygen consumption of *Acroloxus lacustris* in relation to temperature. Above is drawn a Krogh's curve (1914, p. 504) for comparison, the curve being made in this case in a logarithmic scale along the ordinate.

curves above 18° C cannot in this case be due to the influence of a particularly small oxygen content at the end of the experiments; for this oxygen content was, for the big *A. fluviatilis* individuals, on an average 70% of saturation (experiments at about 21°—31° C), and for the small individuals about 81% (experiments at about 21°—36° C), and a diminution of the oxygen content to 70—81% had no influence on the respiration of this species, cp. fig. 4.

The results of experiments with *Ac. lacustris* shown in fig. 7 are too scattered in the case of temperatures below about 12° C, so that a comparison with Krogh's curve cannot be made. If a comparison is made with results at a higher temperature, it will apparently show similar results as for *An. fluviatilis*, viz. that at temperatures above 18° C the percentage increase is smaller than according to KROGH's curve. But in this case the diminished increase may be due to the influence of a smaller oxygen content at the end of the experiments; for this was on an average about 61% of saturation (experiments at about 21°—31° C) and a diminution of this kind in the oxygen content influences the respiration of this species, cp. fig. 5.

7. OXYGEN CONSUMPTION AT DIFFERENT SEASONS OF INDIVIDUALS OF *AN. FLUVIATILIS* AND *AC. LACUSTRIS* OF DIFFERENT SIZE.

The purpose of this investigation is to find the difference — if any — between the oxygen consumption of *An. fluviatilis* and *Ac. lacustris*, when the water in which the animals breathe contains an abundant quantity of oxygen.

It is a well-known fact that species of different sizes have a different respiratory rate, but the relation between respiration and body size has lately been the subject of much discussion and investigation (see e.g. ZEUTHEN, 1947, KLEIBER, 1947, VON BRAND, 1948).

The two species, *An. fluviatilis* and *Ac. lacustris*, are of different sizes. The average weight of the soft tissues of *An. fluviatilis* individuals belonging to the adult groups which have hitherto been subjected to investigations in this work, was about 18—30 mg, whereas the average weight of the *Ac. lacustris* individuals investigated was 5—11 mg. In order to make the oxygen consumption of the two species comparable, the correlation between the oxygen consumption and the body size of the species was examined.

Two series of experiments were carried out at different seasons of the year with each species. The water in which the animals were tested was saturated with air at the beginning of the experiments and the temperature was 16° C.

Ancylus fluviatilis.

Notes on the experiments. The animals were collected mainly in Eskildstrup Møllebæk, Sorø.

1st series: The experiments were carried out in July—August and October—November 1948. In the summer when the lock of the brook is closed the temperature is about 13—16° C (and when the lock is opened about 20° C). In October—November the temperature varied from 10° C to 8.5° C. After collection of the animals they were carried 2 km to the laboratory and were immediately submitted to experiments, which started about one hour after the collection was completed. Each experiment lasted one hour. At the conclusion of the experiments the average air saturation of the water was about 85%.

It has previously been shown (p. 231) that the oxygen consumption of *An. fluviatilis* does not change, if it is subjected to respiration experiments lasting $\frac{1}{2}$, 1, 2, 3, and 6—7 hours, being thereby exposed to declining oxygen contents of the water. Compare also table 1, p. 251. So experiments lasting 1 hour are very suitable to give information about the respiration of this species.

2nd series: The experiments were carried out from November 13th to December 4th, 1950, in the same way, on the whole, as in the first series. The temperature of the brook varied from about 7° C to 3° C. (Among the results are included 2 average values from Nov.—Dec. 49 table 1, p. 251).

The result of the experiments appears in fig. 8a. In this fig. the average weight of the soft tissues per individual is plotted along the abscissa and the oxygen consumption per individual per hour along the ordinate. A logarithmic scale has been used on both axes. As to the representation of the oxygen consumption in relation to weight on a logarithmic scale, see HEMMINGSEN 1933—34, pp. 150, 106 and TETENS NIELSEN 1935, p. 207. If the oxygen consumption is proportional to a fractional power of the body weight we have:

oxygen consumption = $c_1 \times \text{body weight } c_2$, where c_1 and c_2 are constants; and this equation can be brought into linear form by using logarithms:

$\log. \text{ oxygen consumption} = \log. c_1 + c_2 \times \log. \text{ body weight}.$

The representation of the oxygen consumption is given in fig. 8a fol. in relation to the average weight of the individuals, since the values per kg are not comparable when the species compared are of different sizes. If desired, the oxygen consumption per kg live weight may be found by means of the curves in fig. 8a—c. Big individuals of *An. fluviatilis* of 25 mg live weight have for example an oxygen

consumption of about 135—190 ml/kg/hour — when the seasonal variation is taken into consideration — but small individuals of 5 mg live weight have an oxygen consumption of about 170—240 ml/kg/hour. Big *Ac. lacustris* individuals of 10 mg live weight have an oxygen consumption of about 140—200 ml/kg/hour, but small individuals of 5 mg live weight have a consumption of about 170—260 ml/kg/hour.

Thus it is seen that statements of the respiration per kg cannot be considered a rational basis of comparison, as they vary much with the weight of the individuals.

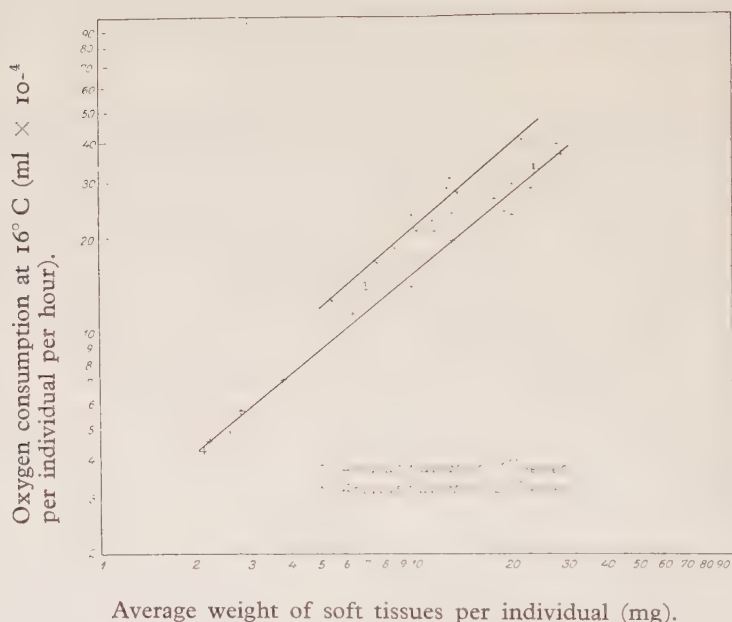


Fig. 8a. Oxygen consumption of *Ancylus fluviatilis* in relation to weight of soft tissues. Experiments at various seasons of the year. The oxygen consumption is shown on the ordinate, and the average weight of the soft parts of the individuals on the abscissa, both on a logarithmic scale.

It is seen from fig. 8a that the oxygen determinations of each series group themselves linearly and that the results of the two experiments are different. The lower line is the regression line of the first series of experiments, the upper line is the regression line of the second series. The oxygen consumption in the series from Nov.—Dec. 1950 is greater than in the series from July—August and Oct.—Nov. 1948. (In the last-mentioned series no difference was observed between the July—Aug. and Oct.—Nov. determinations).

The greater oxygen consumption of *An. fluviatilis* in Nov.—Dec. 1950 than in the earlier series may perhaps be explained by the influence on the animals before the experiments of the different temperatures of the locality. If the animals in winter are adapted to low environmental temperatures by having an increased oxygen consumption, it may explain the seasonal variation found. In Nov.—Dec. the temperatures of the locality were, as mentioned above, about 7° — 3° , and during the earlier experimental period, they were higher — about 13° — 16° (20°) C and 10° — $8,5^{\circ}$ C.

In this connection may be mentioned some poikilothermal marine animals which are acclimatized to low environmental temperatures so that, at certain experimental temperatures, they tend to have a greater oxygen consumption than related species, which are acclimatized to higher environmental temperatures (WELLS 1935, SPÄRCK 1936, THORSON 1936, EDWARDS and IRWING 1943; see also WINGFIELD 1939 and FOX 1939 who both mention conflicting cases).

Acroloxus lacustris

Notes on the experiments. The individuals were collected in the Törkeris Lake and the neighbouring Karls Lake, Hillerød. On the shore immediately after being caught the animals — 35—140 individuals depending upon the weight of the animals — were placed in a respiration bottle of 70 ml, which was filled with aerated water at a temperature of 16° C. A bottle of the same kind was filled with water only. Later on this bottle served to measure the oxygen content of the water before the experiment. As far as possible the animals used in each experiment were of the same size. The two bottles were placed in a Dewar vessel, which acted as a thermostat and contained water at a temperature of about 16° C. The Dewar vessel was placed in a rucksack. Immediately after the beginning of the experiment I cycled to the laboratory. Of course the content of the respiration bottle was shaken on my way to the laboratory. About 20 minutes after the start of the experiments I arrived at the laboratory, the respiration bottle was shaken and $\frac{1}{2}$ hour after the experiment had been started in the field, it was stopped in the laboratory. At the end of the experiments the air content of the respiration bottle was about 92% of saturation.

It has previously been shown (p. 232) that the oxygen consumption of *Ac. lacustris* decreases quickly and considerably in experiments lasting from $\frac{1}{2}$ to 6—7 hours and with decreasing oxygen contents. Consequently a correct — or approximately correct — determination of the oxygen consumption of *Ac. lacustris* must be made immediately after the catching of the animals and in short

experiments, during which only a small decline of oxygen in the water takes place. This has been done as described above.

The 1st series of experiments took place in May and the first days of June, 1949. The temperature of the Törkeris Lake was then about 9.5—16° C. The lake is very much overgrown, muddy and filled up with submerged vegetation; it has a wide reed swamp. Some 25 cm above the bottom the oxygen content of the water was about 69—78% saturated on April 4th, 1949, the temperature 10.4° C.

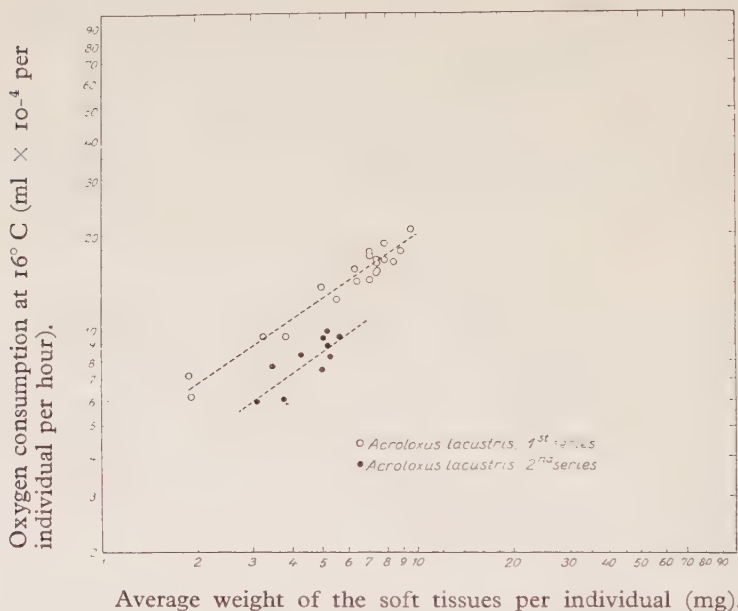


Fig. 8b. Oxygen consumption of *Acroloxeus lacustris* in relation to weight of the soft tissues. Experiments at various seasons of the year.

The 2nd series of experiments were made from the middle of September to the beginning of October, 1950; the temperature of the lake was about 16—13° C.

The results of the experiments are shown on fig. 8b. It is seen that in this case the determinations also group themselves about two straight lines, but the values of the first series are in this case the greater. That the oxygen consumption of the animals is greater in the spring and early summer than in the autumn may be explained by a different physiological state connected with the reproduction of the species. Egg-laying is especially common from May to August.

In this connection it may be mentioned that some marine lamelli-

branchiates have a greater oxygen consumption during the spawning time than at other times (THORSON 1936, p. 115).

But the seasonal variation of the oxygen consumption of *Ac. lacustris* might perhaps also be explained as a result of the influence on the animals of the preceding temperatures of the locality, as in the case of *An. fluviatilis* (p. 243). The temperature of the locality seems to have been somewhat lower during the 1st series of experiments than during the 2nd series.

Comparison between the oxygen consumption of *An. fluviatilis* and *Ac. lacustris* (fig. 8c). It is seen from the figure that the oxygen consumption was found for individuals of both species having a size of about 5—10 mg. If, in this comparison, *Ac. lacustris* individuals with a live weight of about 5—10 mg are compared with individuals of *An. fluviatilis* of the same weight, the question arises whether the latter are young ones or sexually mature, adult animals. The question is of importance; for in a rational comparison the oxygen consumption of the two species, adult individuals of one species must be compared with adult individuals of the other. A comparison between the respiration of adult animals of one species with the respiration of young individuals of another species is of little biological interest.

What is the weight of the soft tissues of the smallest individuals of *An. fluviatilis* which can produce egg-capsules? In order to answer this question individuals of *An. fluviatilis* were placed in a series of small aquaria. The animals were taken from the millbrook, Eskilstrup Møllebæk, Sorø, in August. All individuals in each aquarium were of the same size, but the size varied from aquarium to aquarium. After having produced egg capsules the animals were weighed. The production of egg capsules took place in individuals of the following live weights:

4.2 mg	13.9 mg
4.3 „	14.2 „
7.8 „	26.3 „
8.5 „	27.6 „
11.0 „	33.9 „
12.3 „	

Animals weighing less than 4.2 mg produced no egg capsules. The smallest egg-producing snails of 4.2—4.3 mg produced egg capsules with one egg or without eggs. Snails of 7.8 and 8.5 mg produced egg capsules containing 3—4 eggs. Snails of 12—14 mg produced capsules of 3—5 eggs (in a single case the capsule contained only 1 egg).

It is rather surprising that individuals of *An. fluviatilis* of an average weight of only 4.2—8.5 mg are already sexually mature. They are small animals. The length of their shell-aperture is only about 3.8 and 4.6 mm respectively. For comparison I may state that adult animals of the same population with a live weight of about 30 mg have apertures of about 7.0—7.8 mm.

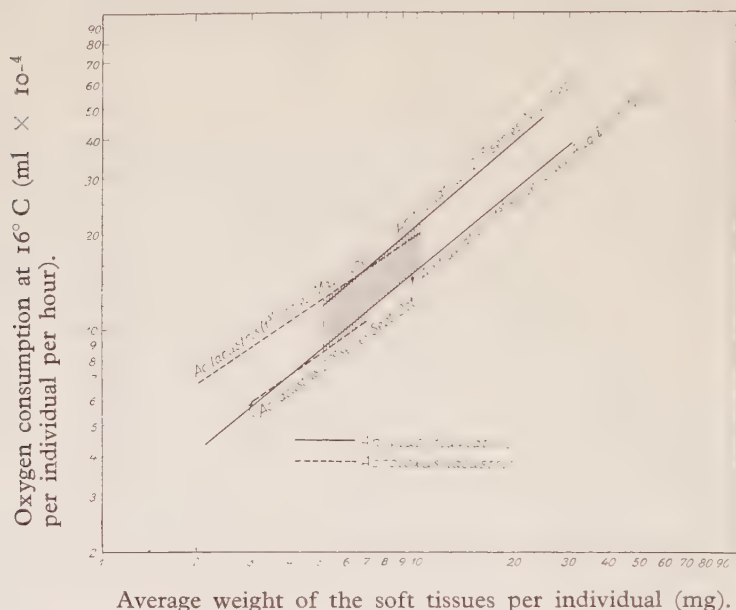


Fig. 8c. Oxygen consumption of *Ancylus fluviatilis* and *Acroloxus lacustris* in relation to weight of soft tissues. Experiments at various seasons of the year. The figure shows the regression lines from fig. 8a and b. The hatched area indicates that the oxygen consumption is of about the same magnitude for those individuals of the two species that have the same live weight.

It is thus found that *Ancylus fluviatilis* individuals are already sexually mature at a weight of the tissues of about 4 mg, even though the capsules at that time are very small. Consequently the above-mentioned *An. fluviatilis* individuals with a weight of 5—10 mg, the respiration of which is to be compared with that of *Ac. lacustris*, must be considered adult animals, and therefore a comparison will be valid:

The varying oxygen consumption — changing according to seasons — of *An. fluviatilis* and *Ac. lacustris* is found to be of about the same magnitude for individuals of the two species having the same live weight of about 5—10 mg (i.e.

adult animals. See the hatched area in the figure). This must be considered a main result of the investigation.

To this may be added that further experiments have to be carried out to test the seasonal variation of the respiration — its magnitude, the possible correlation between reproduction period and oxygen consumption, and between the preceding temperature and the oxygen consumption (acclimatization).

The variation of the oxygen consumption according to the season seems to be different for the two species — as already mentioned; and the variation according to size also differs. As seen in fig. 8c, the increase in oxygen consumption with increasing body weight is greater for *An. fluviatilis* than for *Ac. lacustris*.

At my request a statistician, Mr. H. F. STENBY, C. E., has calculated the regression lines shown in fig. 8a—c of the two series of observations on each species. The formulae of the regression lines were found to be:

for *Ac. lacustris*: $\log y_1 = 0.6210 + 0.6707 \cdot \log x_1$ (1 series)

„ „ „ $\log y_2 = 0.4385 + 0.708 \cdot \log x_2$ (2 series)

for *An. fluviatilis*: $\log y_1 = 0.3782 + 0.8166 \cdot \log x_1$ (1 series)

„ „ „ $\log y_2 = 0.4759 + 0.857 \cdot \log x_2$ (2 series)

It is a reasonable assumption that within each species the regression coefficient c_2 (that is to say, the tangent of the inclination angle of the regression line) is identical or at least nearly the same in both series. A smoothing of the material on this assumption may therefore be of interest. The formulas required and the computation of the relevant standard deviations are given by HEMMINGSEN 1933—34 p. 155—56, see also SNEDECOR 1948 p. 325.

The regression coefficients thus found are 0.674 ± 0.041 and 0.8198 ± 0.0248 for *Ac. lacustris* and *An. fluviatilis* respectively. The difference between the two regression coefficients (0.1458) divided by the standard deviation is 2.899. The probability P that this difference is not due to chance i.e. that it is not zero, can be found by tables which give the probability that any figure is not smaller than t times its standard deviation ("Student"'s t = distribution, see e.g. Fisher and Yates 1943 or Hald 1948).

As a t-value of 2.899 ($f = 52$, f being the degrees of freedom, which is equal to the numbers of observations minus the number of constants that have been calculated from the observations) gives $99.5 < P < 99.9$ %, the probability that the difference might be due to chance is less than 0.5 % in our case.

In other words: the increase in the oxygen consumption of *An. fluviatilis* with increasing weight is significantly greater than the increase in the oxygen consumption of *Ac. lacustris*.

Finally it might be asked: Can the results shown in fig. 8c have an ecological significance, viz. as a contribution to an explanation of the distribution of the two species in nature?

This question refers to 2 facts: (1) that *An. fluviatilis* is limited in its distribution to running water and certain shores with wave-motion, in which environment the oxygen content must in the main be considered high, and (2) that *Ac. lacustris* is chiefly limited to

stagnant water in which the oxygen content must at times be considered low.

The observations shown in fig. 8c and their main result seem unable to furnish an answer to the question since the two species have on the whole the same oxygen consumption for animals of the same weight, 5—10 mg.

8. SOME EXPERIMENTS MADE TO CHECK THE CURVES IN FIG. 8a—b.

A. Has a possible oxygen debt in *Acroloxus lacustris* individuals a perceptible influence on the oxygen consumption shown in fig. 8b?

Against the results stated for *Ac. lacustris* in fig. 8b the objection might be raised that they are too high, because the results are due — at any rate partly — to an actual oxygen debt, which was repaid during the experiments. A similar objection might be made to the high figures in fig. 3 in experiments lasting $\frac{1}{2}$ hour. If this objection were justified, the main result of fig. 8c would be due to momentarily prevailing conditions and not to any characteristic of *Ac. lacustris*.

Considering that *Ac. lacustris* lives on rushes and other aquatic plants some way below the surface in stagnant water and occasionally on stems in some degree protected by leaves, it cannot at the outset be excluded that *Ac. lacustris* lives in water unsaturated with air. If the animals had accumulated an oxygen debt it may have influenced the experiments, since these were started in nature immediately after the animals were caught.

In order to answer the question an experiment was made with *Ac. lacustris* in August 1950. The animals were brought to the laboratory and placed in well aerated lake water for 7 hours. It must be supposed that a possible oxygen debt in the animals would be eliminated after a few hours, as shown for other animals in the following examples. But to be on the safe side the animals were placed in aerated lake water for 7 hours. A still longer time was avoided owing to the possible influence of starvation.

Even if the time used to repay an oxygen debt varies according to circumstances — e.g. the length of the period of deprivation of oxygen — it will be of interest to quote some results of experiments on poikilothermic animals. *Planorbis* required about $\frac{2}{3}$ to $1\frac{3}{4}$ hours to repay an oxygen debt produced during $\frac{1}{5}$ —1 hour of anaerobiosis (BORDEN, 1930, p. 719). *Anodonta*, after an anaerobiosis lasting about 20—25 hours, required a period of about $3\frac{1}{2}$ hours to repay the debt (HERS, 1943, p. 50). In *Mya arenaria* after a period of low tide (anaerobiosis) the period of increased oxygen consumption representing the repayment of an oxygen debt was about 4 hours (VAN DAM 1935). (*Sphae-*

rium corneum requires a recovery period of 4—5 days after 32 days of anaerobiosis, according to the curve given by JATZENKO (1928). But each experiment during the recovery period seems to conclude with an oxygen content below 1 mg per litre of water. This presumably prolongs the recovery periods of the animals).

Chironomus plumosus had an increased oxygen consumption lasting 1—2 hours after a 16 hours' period of anaerobiosis (WALSHE 1947, p. 334 fol.). During oxygen lack grasshoppers build up an oxygen debt. When readmitted to oxygen an increased rate of oxygen consumption occurs, lasting for a period of about 3 hours; the periods of anaerobiosis were about 1¼—2½ hours (BODINE 1928, pag. 397 fol.) A cockroach, *Cryptocercus punctulatus*, took 4 hours to repay a debt (GILMOUR 1940, p. 300). In the common cockroach (*Periplaneta orientalis*) it was found that after 1 hour of anaerobic life at 25° C a period of 3 hours was required before the whole of the oxygen debt had been recovered (DAVIS and SLATER 1926, 1928). A locust, *Schistocerca*, has a distinct oxygen debt after flight. A locust which has been flying for 10 minutes, has an increased metabolism for about 1 hour afterwards; the recovery after prolonged flight takes about 2 hours (KROGH and WEISS FOGH, unpublished).

Very small animals from the plankton, a trochophore larva of *Pectinaria* and a veliger larva of *Mya arenaria*, have short periods of increased oxygen consumption, less than 1 hour (ZEUTHEN 1947, p. 59 fol.), after about 1—3 hours of anaerobiosis.

Thus, at the most, a period of some few hours was enough for the recovery of the oxygen debt in all the cases quoted above.

After the aeration of the water for 7 hours the *Ac. lacustris* individuals were subjected to respiration experiments similar to those

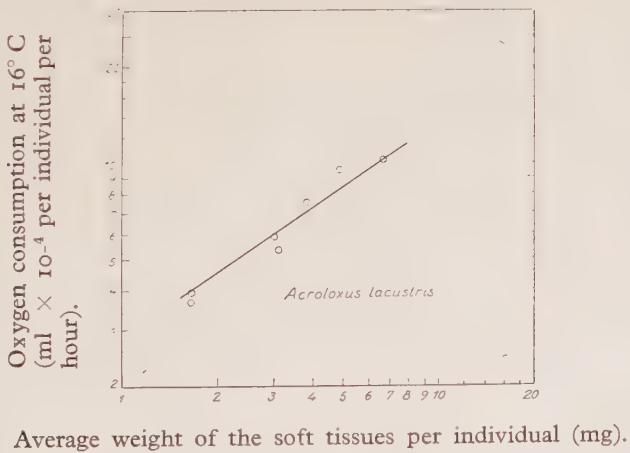


Fig. 9. A comparison between the oxygen consumption of *Acroloxus lacustris* individuals living 7 hours in aerated water before the experiments and untreated individuals put in experiment immediately after catching. The line gives the data of the latter (the same line as in fig. 8b, below), the circles show the results of a series of experiments on the former. The treatment of the animals for 7 hours with aerated water does not diminish their oxygen consumption.

whose results have been shown in fig. 8b: their duration was $\frac{1}{2}$ hour, with a diminution of the oxygen content in the respiration bottles to an average air saturation of about 92%. The temperature during the experiments was 16° C. The animals had been collected in Karls Lake and the neighbouring Törkeris Lake; the temperature of the lakes was about 17° C.

The results of the experiments are shown in fig. 9. For comparison with the observations represented in fig. 9 the lower regression line from fig. 8b is added. This regression line must be regarded as valid during the time of the experiments shown in fig. 9, since the line is a result of other experiments carried out a short time after those on fig. 9.

It is seen that the results of the experiments in fig. 9 do not tend to be significantly lower than the regression line from fig. 8b, but group along this curve.

Thus the experiments have shown that a repayment of a possible oxygen debt preceding the experiments has not caused a perceptible decrease in the results. In other words, it can also be said that the line from fig. 8b shows the oxygen consumption in *Ac. lacustris* without a repayment of an oxygen debt having augmented this consumption.

Thus the objection raised against the results in fig. 8b, and consequently against the main results in fig. 8c, can be dismissed.

B. Will a subjection of *An. fluviatilis* to water deficient in oxygen before the experiments appreciably influence their oxygen consumption?

An. fluviatilis lives in running water, which as a rule must be supposed to be nearly saturated with air, while, as already mentioned, the stagnant water habitats in which *Ac. lacustris* lives, must be supposed at times to be undersaturated. In a comparison between the respiration of the two species immediately after the collection — as made in the experiments, the results of which are represented in fig. 8c — it might be thought that the figures for *An. fluviatilis* would have been higher, if the species had lived in water deficient in oxygen just before the experiments and possibly contracted an oxygen debt.

It has therefore been tested, whether *An. fluviatilis* shows a higher oxygen consumption — under the experimental conditions adopted in this work — after a previous subjection to water poor in oxygen than after having been in oxygen-saturated water.

The experiments were carried out from November 16—December 18. The animals were collected in Eskildstrup Møllebæk, Sorø, and were transported to the laboratory in Hillerød (117 km) in Dewar's vessels. During the season mentioned the temperature of the brook varied from about 7° C to about 3.5° C, and sediment of ochre was

deposited in it. In the laboratory the animals were kept in aerated brook-water of about 15° C. Before the experiments they were placed in water of only about 25—30% of air saturation for 10—24 hours at about 16° C and immediately afterwards subjected to respiration experiments in the usual way. The experiments lasted either half an hour or 1 hour. The control animals were not placed in oxygen-deficient water before the experiments, but were taken directly from the aerated brook-water and placed in the respiration bottles. During the experiments the oxygen contents of the respiration bottles declined to 85—93% of air saturation.

Duration of experiment (hours)	Animals treated with water of low oxygen content (30% air saturation)		Control animals from water saturated with air	
	Live weight (mg)	Oxygen consumption ml hour individual $\times 10^{-4}$	Live weight (mg)	Oxygen consumption ml hour/individual $\times 10^{-4}$
	Average in single experiment	Single experiment	Average in single experiment	Single experiment
$\frac{1}{2}$	10.4	17.4	10.9	23.2
	11.4	18.8	10.1	18.1
	11.4	20.4	10.6	18.0
	9.8	20.2	10.3 \pm 0.16	21.0 \pm 1.70
	10.7 \pm 0.25	18.6 \pm 1.00	10.6	24.5
	10.1	13.6		
	11.3	15.6		
1	10.0	21.2		
	11.3	21.4		
			8.7	18.1
	9.8	15.4	12.6	24.0
	11.6	19.6	11.5 \pm 0.86	22.6 \pm 1.55
	9.1	27.4	12.9	22.1
	11.2 \pm 0.82	21.4 \pm 2.57	10.1	27.5
Mean	11.9	17.0	12.9	21.3
	13.7	27.5		
	10.9 \pm 0.34	19.5	10.9 \pm 0.49	21.8 \pm 1.11

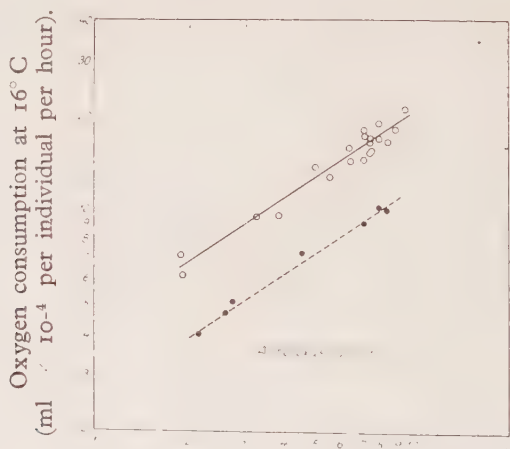
The results of the experiments appear in table 1. It is seen that the *An. fluviatilis* individuals, which have lived for 10—24 hours in oxygen-deficient water at about 16° C, in the ensuing experiments, with the method applied, have no greater oxygen consumption than the control animals. So they have not worked up an oxygen debt which asserts itself perceptibly. It can therefore be concluded that the curve for *An. fluviatilis* would not have been at a higher level, even if the animals had been exposed to oxygen-deficient water in nature, as has possibly been the case with *Ac. lacustris*.

Experiments lasting $\frac{1}{2}$ hour did not give higher average figures for oxygen consumption than experiments lasting 1 hour — in good agreement with the results depicted in fig. 2.

The average respiration figures, 19.5 ± 1.17 and 21.8 ± 1.11 ml/hour/individual $\times 10^{-4}$, found for *An. fluviatilis* of about 10.9 mg live weight — both for animals used for experiments and for control animals — are somewhat higher than the 17.3 ml which can be read in fig. 8a, 1st series, for animals of this size. But they are of the same size as other respiration figures from late autumn and winter, and are included among such in fig. 8a, 2nd series.

C. A comparison between the oxygen consumption of *Ac. lacustris* in experiments lasting $\frac{1}{2}$ hour (oxygen decrease to 91.6% of air saturation) and experiments lasting 1 hour (oxygen decrease to 85.8% of air saturation).

The experiments on *Ac. lacustris*, the results of which are shown in fig. 8b & c, were, as already mentioned, carried out in $\frac{1}{2}$ hour and



Average weight of the soft tissues per individual (mg).

Fig. 10. Rate of oxygen consumption at 16° C of *Acroloxus lacustris* in relation to weight of soft tissues. The duration of the experiment is $\frac{1}{2}$ hour in the upper series (white circles) and 1 hour in the lower series (black circles).

immediately after catching the animals. But as shown in fig. 3, the extent of the respiration of this species under the given conditions depends upon the duration of the experiments and the diminution of the oxygen content during the experiment. It might therefore be supposed that these circumstances could influence big and small individuals of *Ac. lacustris* in a different way, and this would consequently be of importance for the magnitude of the gradient of the curve for *Ac. lacustris* in fig. 8b & c.

In order to test whether the conditions of the experiments affect small and big individuals of *Ac. lacustris* in a different way a series of experiments lasting 1 hour was carried out and the results of this series were compared with the series of experiments lasting $\frac{1}{2}$ hour (fig. 10). The series lasting 1 hour comprised individuals of various sizes like the series lasting $\frac{1}{2}$ hour, and the animals were caught in the same locality, Törkeri Lake. At the conclusion of the experiments lasting 1 hour the average oxygen content was 85.8% of air saturation.

It is seen from fig. 10 that the experiments lasting 1 hour showed a smaller oxygen consumption — as might be expected — and also that the results group themselves along a straight line, which has the same gradient to the abscissa as the line of the experiments lasting $\frac{1}{2}$ hour. That is to say that small and big individuals of *Ac. lacustris* have been influenced in the same way by an increase of the duration of the experiments from $\frac{1}{2}$ hour to 1 hour, and by the decrease in the oxygen content which accompanies the increase in the duration of the experiments.

D. Do adverse aquarium conditions influence the oxygen consumption?

Specimens of *Ac. lacustris* collected in Karls Lake and Törkeri Lake at the beginning of October were kept in an aquarium for about a month at about 15° C. The water was aerated. The animals were mostly found on the glass-walls, which were covered with a layer of microscopical green algae. Even if the snails had eaten some algae, many of them were dead after a month in the aquarium. The cause of death was possibly starvation, since the other animals, which were still alive, had considerably lost weight.

In consequence of adverse conditions most of the animals still living were immovable and "encysted", that is to say, a secretion forming a lid covered the whole aperture of the snail-shell. The oxygen consumption of these individuals was found in the usual way: the duration of the experiments was $\frac{1}{2}$ hour, the temperature during the experiment 16° C and the oxygen content of the water after the experiment about 92% of air saturation or more.

The result of the experiment is shown in fig. 11, in which also the lower regression line from fig. 8b, valid at the time of the experiments,

has been drawn. It is seen that the individuals of *Ac. lacustris*, that lived under adverse aquarium conditions for about a month, had a very low oxygen consumption, $\frac{1}{2}$ to $\frac{2}{3}$ that of animals just collected in nature.

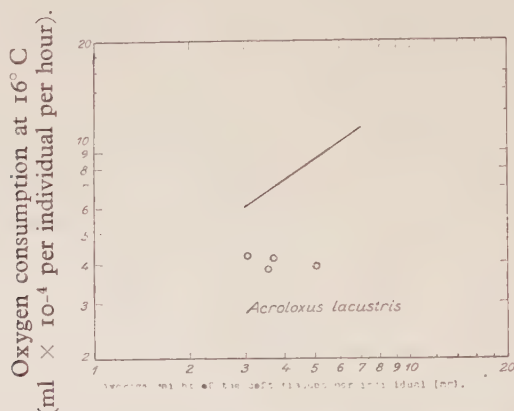


Fig. 11. Oxygen consumption of individuals of *Acroloxus lacustris* which lived about 1 month in an aquarium under adverse conditions and possibly suffered from starvation. For comparison the lower regression line shown in fig. 8b is also drawn.

E. The oxygen consumption of *An. fluviatilis* and *Ac. lacustris* found in experiments in a respiration chamber with running water.

In the respiration experiments hitherto described in this work the animals were placed in closed respiration bottles, in which the oxygen contents decreased during the experiments. The decrease of the oxygen content was small, only to about 85—92% of air saturation unless otherwise stated.

An objection to the results shown in fig. 8a—c might possibly be that the decrease in the oxygen content itself might be a stimulating factor, which involved an alteration in the extent of the respiration.

In order to examine this possibility some experiments were carried out in an apparatus through the respiration chamber of which water flowed during the experiments, and in which the animals therefore were under a constant oxygen pressure as long as the experiments lasted. The oxygen content of the water before and after passing the respiration chamber was measured, the speed of the current was measured, and from these two measurements the oxygen consumption was calculated. The apparatus was constructed by Mr KAY BRUNFELDT, M. Sc. and will be described later on. The result of the measurements, which Mr. BRUNFELDT has been so kind as to make in collaboration with me, were:

An. fluviatilis. The oxygen consumption found was 13.8×10^{-4}

ml O_2 /hour/individual at $16^\circ C$. and remained the same during 1 hour 48 min. The average weight of the individuals was 9.6 mg and the oxygen content of the respiration water after the experiments 92.6% of saturation. The figure 13.8 does not differ considerably from the 14.5 ml which can be read on the curve in fig. 8a, 1st series, for animals of the size mentioned.

Ac. lacustris. The oxygen consumption found was 14.4×10^{-4} ml O_2 /hour individual at $16^\circ C$ and remained the same during 1 hour. The average weight of the individuals was 6.7 mg and the oxygen content of the respiration water after the experiment was 84.3% of air saturation. Nor does the value 14.4 ml differ essentially from 15.2 ml, which can be read on the curve of fig. 8b, 1st series, for animals of the size mentioned for this species.

Since the oxygen consumption of *Ac. lacustris*, as shown above (fig. 5), varies with the oxygen concentration, even if the latter is near saturation, the 14.4×10^{-4} ml O_2 individual which was found, would increase, if the oxygen content after the experiment was changed from 84.3% to 91.6% of saturation; the last mentioned figure is the final degree of saturation in the *Ac.* experiments shown in fig. 8b. A certain — but doubtful — estimate of how much this increase may amount to can be formed through application of the curve in fig. 5 for an oxygen content of the water of about 5—6 ml. Such a calculation will give an oxygen consumption of 16.5 ml O_2 /h/individual for *Ac. lacustris*. As might be expected, this value does not differ much from the 15.2 ml O_2 individual, which the curve in fig. 8b, 1st series, shows for *Ac. lacustris* individuals of a weight of 6.7 mg.

The objection discussed can therefore be dismissed.

During the experiments with animals in the respiration chamber with running water it was observed that many individuals of *Ac. lacustris* moved in the direction of the flow as far as possible, but *An. fluviatilis* remained still.

A comparison between the results of the tests in the respiration chamber with running water and some of the other, earlier results may also be carried out — e.g. the consumption of *An. fluviatilis* shown in fig. 2 and found in experiments of a duration of 1—5 hours: about 130 ml/kg/hour. Since these animals had an average weight of about 20.9 mg and the animals in the control experiment (with respiration chamber with running water) the weight of 9.6 mg, the first-mentioned would have the oxygen consumption:

$$\frac{130 \times 20.9}{10^6} \times \left(\frac{9.6}{20.9} \right)^{0.82} = 14.1 \times 10^{-4} \text{ ml/individual/hour, if they}$$

had the average weight of the last-mentioned. It agrees with the 13.8×10^{-4} ml/individual/hour found in the experiment with running water in the chamber.

According to fig. 3 the oxygen consumption of *Ac. lacustris* is about 285 ml/kg/hour in experiments of a duration of $\frac{1}{2}$ hour. Since the average weight

of the animals in these experiments was about 5.4 mg and in the control experiment (with respiration chamber with running water) was 6.7, the oxygen consumption of the first-mentioned would be $\frac{285 \times 5.4}{10^6} \times \left(\frac{6.7}{5.4}\right)^{0.67} = 17.7 \times 10^{-4}$ ml/individual/hour, if they had the average weight of the last-mentioned. This number is a little greater than the 14.4×10^{-4} ml/individual/hour found in the control experiment with a respiration chamber with running water. But considering the steep decrease found in experiments of short duration (see fig. 3) one cannot presumably expect complete agreement.

9. SURVIVAL UNDER ANAEROBIC CONDITIONS.

The literature contains certain statements concerning the reactions of *An. fluviatilis* and *Ac. lacustris* to oxygen-deficient or oxygen-free water. Thus ANDRÉ (1893, p. 450) writes: "mais si l'eau ambiante ne contient plus assez d'oxygène ils viennent à la surface et font saillir une partie de leur corps dans le but d'imprégner d'air l'eau adhérent à leur tégument et de satisfaire ainsi aux besoins de la respiration. Cela, se rapporte aux *Ancylus fluviatilis*; quant aux *A. lacustris*, ils peuvent demeurer impunément assez long temps dans une eau mal oxygénée; j'en ai conservé jusqu'à 15 jours, sans les laisser à la surface dans un petit bocal dont l'eau n'a pas été changée pendant tout ce temps". ANDRÉ also remarks that he has kept *Ancylidae* alive for 4 or 5 days in boiled water, but he does not mention which species he treated in this way.

NILS HJ. ODNER (1941, p. 15), as previously mentioned, states that *Ac. lacustris* is almost insensitive to oxygen lack and, moreover, is able to live in water which has been made oxygen-free by boiling. Furthermore he says that *An. fluviatilis*, which requires fresh water in aquaria, can often be seen above the surface of the water, obviously because of a lack of oxygen.

TORSTEN GISLÉN (1945), as already stated, is of the opinion that *An. fluviatilis* requires well-circulated water and abundant oxygen.

B. HUBENDICK (1947) writes about *An. fluviatilis*: „Das die Art normaliter an fließendes Wasser gebunden ist, könnte man annehmen, dass sie hohen Sauerstoffgehalt des Wassers fordert. Ihr Vorkommen in einigen wenigen Flachlandsseen, deren Sauerstoffgehalt im Winter stark herabgesetzt sein muss, zeigt, dass dieser Bedarf nicht begrenzend zu wirken braucht, wenigstens nicht im Winter". As to this, it must be said, however, that *An. fluviatilis*, as far as is known, when it occasionally occurs in lowland lakes, is only found in the littoral zone. But it is not correct to say that the oxygen in this zone must be greatly diminished in the winter. Thus the occurrence of *An. fluviatilis* in the littoral zone in some few lakes cannot tell us

whether the oxygen requirement of the species does not tend to limit its occurrence.

It will be seen from the above quotations that the views put forward need the support of more exact information. A comparative experiment has therefore been made to ascertain how long the two species, *An. fluviatilis* and *Ac. lacustris*, are able to survive under anaerobic conditions.

The experiments were carried out in February. The *An. fluviatilis* were once more taken in Eskildstrup Møllebæk, Sorø, and the *Ac. lacustris* individuals in Törkeris Lake, Hillerød. The temperature of the water in the daytime was then only a few degrees centigrade. After the collection the animals were left to stand for 24 hours at a temperature of about 13° C, before they were subjected to the experiments.

20 individuals of each species were placed in bottles of about 100 ml. The bottles were filled with water, which had been treated with nitrogen, so that it only contained about 0.5—0.10 ml O₂ per litre. The bottles were wrapped in black paper and placed in a water-bath at a temperature of about 18—20° C in the daytime and about 12° C at night.

A series of 7 bottles was set up for *An. fluviatilis*. For *Ac. lacustris* a series of 6 bottles was first set up, then a series of 9 bottles. After some time a bottle was opened, and it was ascertained how many animals were still alive.

The result of the experiment appears in fig. 12. It will be seen that almost all *An. fluviatilis* individuals keep alive for the first 24 hours,

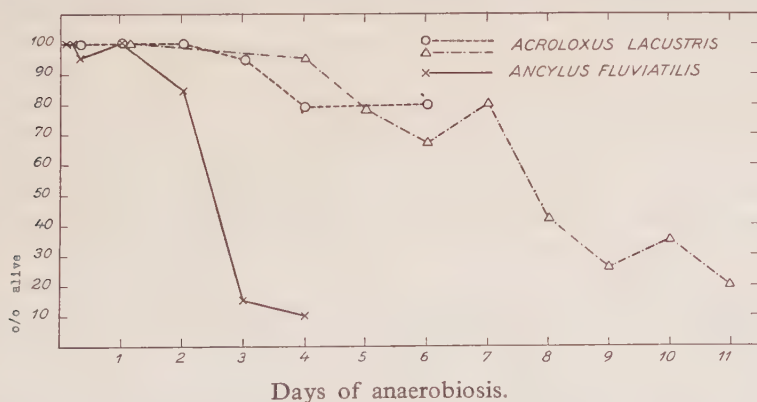


Fig. 12. Duration of life of *Acroloxus lacustris* and *Ancylus fluviatilis* under anaerobic conditions.

which surprised me, but nearly all *Ac. lacustris* survive for 3 days or more. 50% of the *An. fluviatilis* individuals are alive after 2 or 3

days; the same is the case with *Ac. lacustris* after 7 or 8 days. 10—15% of the *An. fluviatilis* individuals are still alive after 3 or 4 days. 20—35% of the *Ac. lacustris* individuals are alive after 9 or 11 days. So the experiment obviously showed that *An. fluviatilis*, the species from running water, has not the same capacity to survive under anaerobic conditions as *Ac. lacustris*, the species from still waters. Thus this experiment agrees very well with the distribution of the two species in nature, since the species from running aerated water has turned out to be the more sensitive to oxygen lack.

Perhaps the difference between the two species in regard to survival during periods of oxygen lack may be correlated with a difference in substances from which the animals can derive energy during these periods. In order to try this possibility Mr. KAY BRUNFELDT kindly analyzed some *An. fluviatilis* and *Ac. lacustris*, collected in January and December respectively. The snails were analyzed for content of glycogen and nitrogen; the nitrogen value multiplied by 6.25 gave the content of protein. 100 minus the percentages of glycogen and protein gave the percentage of "fat" etc.

The results of these analyses and calculations were the following average percentages calculated in regard to the dry weight of the animals:

	Protein. %	Glycogen. %	"Fat" etc. %
<i>An. fluviatilis</i>	54 ± 5.7	5.8 ± 0.53	38 ± 5.1
<i>Ac. lacustris</i>	49 ± 6.9	12.7 ± 0.61	40 ± 6.4

It is seen that the protein and fat differences are small and doubtful, but the glycogen content of *Ac. lacustris* is about twice as large as in *An. fluviatilis*. Since glycogen is among the polysaccharides most commonly utilized during oxygen lack (cp. e.g. von BRAND 1946 p. 177) the observed ratio is in good accordance with the survival difference of the two animals under anaerobic conditions.

10. MOVEMENTS IN WATER DEFICIENT IN OXYGEN.

In nature it is sometimes seen that *An. fluviatilis* individuals gather at the surface of the water on stones projecting above the water. This might be due to a need for fresh, aerated water. In aquaria with water of a low oxygen content it was at any rate observed that the animals ascended to the surface of the water, but not above it (cp. BERG 1948, p. 197). Previously it was not known how *Ac. lacustris* moved in oxygen-deficient water. There might be a difference between the movements of the two species in an anaerobic environment; B. SHARP (1883, p. 4) makes a suggestion to that effect: „Ist das Wasser jedoch nicht frisch und gewechselt worden, so kommt *Ancylus fluviatilis* unfehlbar früher oder später an die Oberfläche. Bei *Ancylus lacustris* ist das nicht so constant." Therefore some expe-

riments were made on the movements of the species in water deficient in oxygen, and in water containing plenty of oxygen, in the following way:

In July 10 *An. fluviatilis* and 10 *Ac. lacustris* were placed in each of 3 aquaria. Water nearly oxygen-free (through which was bubbled N₂ for more than 1 hour) was poured into aquaria 1 and 2. Aquarium 3 served as a control, being filled with water which had been aerated with atmospheric air. At the beginning of the experiment all the animals were lying at the bottom of the aquaria, which had a height of 16 cm. The aquaria were filled with water and covered with glass-lids, so that there was no air above the water in the aquaria.

Was there any difference between the movements of the animals in the aquaria with deoxygenated and aerated water? Was there any difference between the movements of the two species?

	— oxygen Data from aquaria 1 and 2		+ oxygen Control aquarium 3		
	An. fluv.	Ac. lac.	An. fluv.	Ac. lac.	
exp. 1					
15 hours	17	8	3	2	Upper half
after					
start	3	12	7	8	Lower half
exp. 2					
21 hours	12	4	3	0	Upper half
after					
start	8	16	7	10	Lower half

Table 2. In aquaria with water deficient in oxygen most individuals of *An. fluviatilis* climb to the upper half, whereas most *Ac. lacustris* individuals stay at the bottom.

The results of the experiment are shown in table 2. It is seen that in the aquaria with water devoid of oxygen, most of the individuals of *An. fluviatilis* climbed to the upper half, but most of the *Ac. lacustris* individuals stayed at the bottom. In the control aquarium with abundant oxygen the greatest number of animals of both species remained at the bottom. A repetition of the experiment gave in the main the same result: in water deficient in oxygen, *An. fluviatilis* has a stronger tendency to climb upwards than *Ac. lacustris*.

11. CONCLUDING REMARKS.

The observations on the Ancyliidae will here be recapitulated and discussed in connection with similar results concerning other fresh-water animals.

How do the Ancyliidae breathe? This question has previously been the subject of many investigations and reflections. E. ANDRÉ (1893, p. 445) takes a historical survey of the literature dealing with these problems, and he sums up his own anatomic investigations and the results of those of others as follows (l. c. p. 452): „il n'y a pas de cavité pulmonaire. Il n'y a pas d'organe spécialement adapté à la respiration. La respiration se fait en grande partie par le bourrellet palléal et un peu par le lobe auriforme. Le lobe auriforme n'est pas une branchie, mais l'homologue de l'appendice pneumostome des Physes et des Planorbes. L'animal respire l'air dissout dans l'eau." So according to ANDRÉ Ancyliidae are pulmonary snails without lungs; they utilise the oxygen of the water and have no gills. But it is still stated that these animals possess a gill (e.g. BOETTER 1944, p. 266).

The oxygen consumption of animals from running and stagnant water. It has been found by FOX and SIMMONDS (1933) that the oxygen consumption of the nymph of the ephemerid *Baëtis rhodani*, living in a swift stream, is 3—4 times that of *Chloëon dipterum* from a pond. Further that the larva of the trichopterid *Hydropsyche* sp. from a swift stream has an oxygen consumption which is $1\frac{1}{2}$ times that of *Molanna* sp. from a pond. "The oxygen consumption of individuals of *Asellus aquaticus* from a swift stream is $1\frac{1}{2}$ times that of the same species from a slow stream."

Results of a similar kind have been obtained with several Ephemeroptera-nymphs. The oxygen consumption of nymphs of *Ephemerella ignita* is 3 or 4 times that of *Caenis* sp. nymphs. Their habitats are a stream and a pond respectively. The oxygen consumption of the big nymphs of *Ecdyonurus venosus*, *Ephemera danica* and *E. vulgata* decreases in the order mentioned. They live under stones in a swift stream, burrowing in sand in a stream, and burrowing in mud in a pond respectively (FOX, SIMMONDS and WASHBOURN, 1935).

ET. HUBAULT (1927, p. 193) has made a survey of literature concerning the oxygen consumption of organisms from running water. He has also carried out comparative experiments on the oxygen consumption of the ephemeropteran nymph *Epeorus* sp. from swiftly running water, and on *Ephemera vulgata* from ponds and the lower reaches of brooks. He finds that the *Epeorus* nymph uses about 2.0—2.8 times as much oxygen per gram per 24 hours as the *Ephemera*

vulgata nymph. The *Epeorus*-nymphs weighed only about 0.26—0.44 of the weight of the *Ephemera* larvae. It is not known how the oxygen consumption of these animals changes when the weight of the animals varies; but if they follow Rubner's surface law, the *Epeorus*-nymphs should use about 1.6—1.4 times as much oxygen per gram as the *Ephemera*-nymphs. Thus they may perhaps use somewhat more oxygen than accounted for by the difference in size alone.

As stated in the introduction, it has been found for chironomids that 2 species from running water have higher metabolic rates in aerated water than 2 closely related species from still water (WALSHE, 1948). The fact that according to WALSHE (1948, p. 40) relatively high metabolic rates have also been found in stream species of other aquatic arthropods suggests that this property may be a general characteristic of animals living in streams. This rule, which is based on valuable and convincing experiments with arthropods, is not so general, however, that it comprises the two molluscs investigated in this work, *An. fluviatilis* and *Ac. lacustris*. In this case an oxygen consumption is found, varying according to the season, but of the same magnitude for both species (for individuals having the same live weight), a result I did not expect to find.

The oxygen consumption in relation to the oxygen-concentration of the water. Some Ephemeroptera-nymphs from running water belonging to the genus *Baëtis* have an oxygen consumption which falls immediately when the oxygen in the water decreases, whereas the oxygen consumption of *Chloëon dipterum*, a species from still waters, does not decrease until the oxygen has fallen below one fifth air saturation (FOX, WINGFIELD & SIMMONDS 1937, p. 210). The oxygen consumption of two chironomid species, *Tanytarsus brunnipes* and *Anatopynia nebulosa*, living in streams also falls as the oxygen content of the water diminishes, whereas that of two closely related still-water species, *Chironomus longistylus* and *Anatopynia varia*, remains approximately constant until the oxygen content has fallen to a low value (WALSHE, 1948).

On the other hand, it has also been found that the oxygen consumption of *Baëtis scambus* — a species from flowing water — is almost independent of the quantity of oxygen in the water, both below and above air saturation (FOX, WINGFIELD & SIMMONDS, l. c. p. 212).

Thus several, but not all animal species from running water, hitherto investigated, vary their oxygen consumption in close correlation with alterations in the oxygen content of the water.

Two experiments illustrating these conditions were made with *An. fluviatilis* and *Ac. lacustris*:

If *An. fluviatilis* and *Ac. lacustris* are subjected to respiration experiments of increasing duration and therefore decreasing final values of the oxygen concentration, a characteristic difference between the species is seen. *An. fluviatilis* has such a stable respiration that it is able to maintain this for a long time in spite of low final values of oxygen content, whereas *Ac. lacustris* already in experiments lasting only $1\frac{1}{4}$ hours and with a final oxygen content of 69% of air saturation shows a clear decrease of the oxygen consumption per kg per hour (cp. p. 231 fol.).

If respiration experiments of a duration of 1 hour are carried out in water with oxygen contents varying from experiment to experiment (but only decreasing slightly in each experiment cp. p. 235 fol.) a corresponding characteristic difference is seen in the two species in their dependence on the oxygen content of the environment (figs. 4 and 5): *An. fluviatilis* has a constant oxygen consumption of about 135 ml/kg/hour at 16° C, even if the oxygen content falls to about 3 ml per litre of water, that is to say, far below air saturation, whereas the oxygen consumption of *Ac. lacustris* sinks as soon as the oxygen content of the water falls below about 6 ml per litre.

As *An. fluviatilis* is a species from flowing water and *Ac. lacustris* is found in still water, it might have been expected that the former — like some of the insect larvae — would be less stable and the latter more stable in regard to respiration when the oxygen content is small. But here again it is seen that these two snails do not conform to the rule which has been found for arthropods.

The oxygen consumption in relation to temperature. Ephemeropteran nymphs from slow-flowing water or still waters had a greater heat tolerance than those from swift streams, and these differences were correlated with greater temperature fluctuations in the former environments (WHITNEY, 1939). It has also been shown that larvae of stream chironomids are less resistant to high temperatures than still water forms, and in accordance with this it was found that the temperature in the stream never rose above 15° C during the summer, whereas a water temperature of 20° C was recorded in the still-water habitats (WALSHE 1948).

An. fluviatilis and *Ac. lacustris* were examined to find whether the relation between respiration and temperature showed differences which might be connected with their occurrence in cool, running waters and warm still-waters respectively. It is a well known fact that the respiration of an animal increases with the temperature, until at certain high temperatures it suddenly falls abruptly. In *An. fluviatilis* and *Ac. lacustris* it appeared that the respiration rose with the temperature to 32°—34° C and about 31° C respectively. It then fell quickly. Thus the running water species has no

lower temperature maximum than the species from still-waters.

Survival of animals from running and still water under anaerobic conditions or in water deficient in oxygen. It has been shown that nymphs of the ephemeropteran *Baëtis rhodani* living in a swift stream, are more sensitive to oxygen lack than nymphs of *Chloëon dipterum*, from a pond, and likewise that the trichopterid *Hydropsyche* sp. from a swift stream is more sensitive to oxygen lack than *Molanna* sp. from a pond (FOX & SIMMONDS, 1933, FOX, SIMMONDS & WASHBOURN 1935).

WALSHE (1948) has compared chironomid larvae from running water and stagnant water. Of the larvae of ten chironomid species, those from streams are much less resistant to anaerobic conditions than those from still water.

As regards the two Ancyliidae the experiments in this field have given similar results as for the above-mentioned arthropods. It has turned out that *An. fluviatilis*, the species from running water, has not the same capacity for survival under anaerobic conditions as *Ac. lacustris*, the species from still water.

The movements of the two species of snails in deoxygenated and in oxygenated water agree very well with the observed difference in the capacity to survive under anaerobic conditions: *An. fluviatilis* shows a greater tendency to climb upwards towards the oxygen of the air than *Ac. lacustris*.

Altogether we are confronted with the unexpected result that the oxygen consumption of *An. fluviatilis* is found to be of the same magnitude as the consumption of *Ac. lacustris* (in both cases varying according to the season); that *An. fluviatilis* maintains a more stable oxygen consumption under deficiency of oxygen than the latter, but that nevertheless *An. fluviatilis* dies more quickly under anaerobic conditions than *Ac. lacustris* and has a greater tendency to climb upwards in deoxygenated water. We are thus obliged to accept the fact that the two species differ in powers of resistance to anaerobic conditions although they have an oxygen consumption of the same magnitude (varying over the same range).

The greater sensitivity of the stream species is of course in good accordance with its distribution in waters with plenty of oxygen. But it is impossible to explain the distribution of the two species in nature by means of their respiration requirements. Therefore the present studies on the two snails show that in ecology it is dangerous to draw conclusions as to the requirements of the animals exclusively from the characteristics of the environment. The ecological hypotheses deduced from observations in nature must often be verified by experiments.

Remarks on the height of the shells of the species and their distribution. As mentioned in the introduction, the species from running water have a high shell, and the species from still water a low shell, although the opposite might perhaps be expected. However, BOETTGER (1933, p. 362) is of the opinion that *Ac. lacustris* derives advantage from its low shell in still water, when attached to a rush which sways in the wind, „denn die napfförmige Schale bietet zweifellos der Bewegung im Wasser weniger Widerstand, als wenn sie in Windungen hoch aufgebaut wäre.“ Even if this statement perhaps is correct it is of no significance, and the problem concerning the distribution of the two species in spite of their form remains.

Exceptionally the two species *An. fluviatilis* and *Ac. lacustris*, may be seen in nature beside each other. This is the case in a locality in the river Susaa (BERG 1948, p. 196). HUBENDICK (1947, p. 481), too, mentions an example of the contemporary occurrence of the two species in running water.

In the Møllebækken, Eskildstrup, near Sorø, some few *Ac. lacustris* have sometimes been found together with a large population of *An. fluviatilis*. But no independent population of *Ac. lacustris* develops in the brook. Obviously the individuals are carried to the brook now and then from the millpond above.

In certain cases *An. fluviatilis* lives in lakes, presumably always on stones in the wave-washed zone. BROCKMEIER (1896) has found it in a lake, Pulvermaare in Eiffel; GEYER (1926, p. 151) states that a special lake-form, *capuloides* Porro, lives in the lakes in Northern Italy, Switzerland, in Starnberger and Chiemsee. GISLÉN (1945) and HUBENDICK (1947, p. 458) mention the species from Swedish lakes, e.g. from Vättern. The distribution of *An. fluviatilis* in Ringsjön, Scania, and the brooks flowing into this lake is described by HALL (1949); the possible influence of the Calcium content and pH is considered. The species has also been found in 4 Danish lakes in the central part of Jutland (ISAGER and P. NIELSEN 1923, CARLO F. JENSEN and E. W. KAISER leg. (KAISER, 1950)); it always lives in the stony, wave-washed zone of these lakes. It is not known why it only occurs in some few Danish lakes.

12. SUMMARY

1. For several arthropods previous authors have found that stream species use more oxygen than stagnant water species. This is not the case with *Ancylus fluviatilis*, a stream snail, and *Acroloxus lacustris*, a stagnant water snail: The oxygen consumption of the two species is found to be of about the same magnitude and varying, according to the season, within about the same range (fig. 8c, p. 246). The char-

acter of this seasonal variation is still unknown (p. 247). The compared individuals are of the same size and are adult animals, so the comparison is valid.

2. The above-mentioned main result has been controlled in several ways:

a) It has been shown that no part of the oxygen consumption of *Acroloxus lacustris* is due to the repayment of an oxygen debt.

b) It has been shown that the oxygen consumption of *Ancylus fluviatilis* is not increased even if the species lives many hours in water deficient in oxygen (only about 30% air saturation).

c) Furthermore it has been verified that the oxygen consumption of some individuals of *Ancylus fluviatilis* and *Acroloxus lacustris* remains almost as shown in fig. 8a & b (1. series) in a respiration chamber with running water.

3. With increasing body weight the oxygen consumption of *Ancylus lacustris* increased more rapidly than that of *Acroloxus lacustris* (fig. 8c, p. 246).

4. The oxygen consumption of the stream species *Ancylus fluviatilis* remains approximately constant, until the oxygen content of the water has fallen to a low value, whereas that of the stagnant water species, *Acroloxus lacustris* falls as the oxygen diminishes (figs. 2 and 3, p. 231-232, figs. 4 and 5, p. 235-236).

This is the opposite of what has been found for some stream and stagnant water arthropods.

5. A short period of starvation (about 5½ hours) before the experiments does not diminish perceptibly the oxygen consumption of *Ancylus fluviatilis* or *Acroloxus lacustris*.

6. Individuals of *Acroloxus lacustris* that lived under adverse aquarium conditions (presumably starving) for about a month, had a very low oxygen consumption, much lower than animals just collected in nature (fig. 11, p. 254).

7. The maximum temperature (about 31° C) which the stagnant water species, *Acroloxus lacustris*, will tolerate before the respiration is disturbed, is not higher than that which the stream species, *Ancylus fluviatilis*, can endure.

8. *Ancylus fluviatilis* has not the same capacity to survive anaerobic conditions as *Acroloxus lacustris* (fig. 12, p. 257). This result agrees well with the fact that the former is a stream species, the environment of which generally abounds in oxygen, and the latter is a stagnant water species, the environment of which may now and then be poor in oxygen.

9. *Ancylus fluviatilis* has a greater tendency than *Acroloxus lacustris* to climb upwards towards the surface of the water when the water is deficient in oxygen.

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Der Vihtajärvi.

Ein durch die Abwässer einer Pulverfabrik azidotrophierter See.

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Die vorliegende Untersuchung wurde von dem AB Central-laboratorium (Chemie) und mir (Biologie) zwecks eines Gutachtens über die Art und den Umfang der Schäden, die durch die Abwässer einer grossen Dynamit- und Pulverfabrik im See Vihtajärvi, der ihr Wasser teilweise aus diesem See empfangende Bucht Vihtalahti des grossen Leppävesi und in den angrenzenden niedrigen Ufergebieten verursacht werden, ausgeführt. Da die Ergebnisse teils auch rein limnologisch ein gewisses Interesse bieten, mögen sie hier für den betreffenden Teil mitgeteilt werden.

Ich bitte in diesem Zusammenhang Herrn Dr. B. Nybergh, dem Direktor des Zentrallaboratoriums, der mir gütigst die chemischen Data zur Verfügung stellte, zu danken.

Um Vergleichspunkte zu erhalten, möge zunächst die Limnologie der in der Nachbarschaft der Vihtajärvi liegenden und von der Fabrik nicht beeinflussten Seen Kuhajärvi und Siikajärvi kurz berührt werden.

Das Felsengerüst um den *Kuhajärvi* besteht aus Granit. Die Erdarten sind vorwiegend Moräne und Sand. Ton ist ziemlich wenig vorhanden und Moorböden fehlen. Die Gegend ist einigermassen beackert und angesiedelt. Keine grösseren Zuflüsse. Abfluss nach dem Leppävesi. Die höhere Wasservegetation ist mit einigen Ausnahmen im allgemeinen licht oder fehlend und in erster Linie aus *Equisetum limosum*, *Phragmites communis* und *Potamogeton*-Arten zusammengesetzt.

Der Chemismus wurde im grossen ganzen ähnlich derjenigen der oligotrophen s.str. 1) Seen gefunden. Das elektrische Leitvermögen, die Alkalinität und besonders das pH waren jedoch höher als in diesen Gegenden insgemein. Trotzdem der See am 27.VI.1950

1) D.h. nicht dystrophen.

schon eine Temperaturschichtung zeigte, war der O_2 -Gehalt auch in den tieferen Wasserschichten hoch.

Die Seefarbe war am 20.VI.1950 grün und die Wasserfarbe 20 Pt mg/l. Am selben Tage betrug die Sichttiefe des etwas trüblichen Wassers etwa 2.25 m.

Unter den Phytoplanktern ¹⁾ traten (siehe Tab. 1) am 20.VI.1950 *Fragilaria crotonensis* und, besonders bezüglich des Volumens, *Asterionella formosa* (ungewöhnlich grosswüchsig) entschieden dominierend auf. Die nächstgrösste Rolle spielten *Dinobryon* mit *D. bavaricum* an der Spitze und *Cyclotella stelligera*. Die Zahl der Arten war relativ gering, nur 25, vorwiegend Diatomeen und Chrysomonaden.

Quantitativ war das Vorherrschen der Diatomeen noch schärfer ausgeprägt, indem ihr Anteil von dem ganzen Phytoplanktonvolumen etwa 90 % ausmachte. Die Volksdichte betrug etwa 186000 Einheiten/l oder im Volumen — bei Annahme einer im grossen und ganzen gleichmässigen vertikalen Verteilung im oberen Epilimnion — in einer 1 m dicken Schicht etwa 4.2 l/ha. Auch im Hinblick darauf, dass man es mit Wasserproben zu tun hat, war die Zahl der Zooplankterarten ziemlich gering: nur 3 Ciliaten und je 2 Rotatorien und Cladoceren. Die Volksdichte war ebenfalls verhältnismässig niedrig: etwa 1700 Individuen/l, entsprechend etwa 30.2 l/m³.ha.

Die Planktongemeinschaft war im Sinne THUNMARK's eine protoccalenartenarme—desmidienartenfreie *Asterionella formosa*—*Daphnia cristata*—Gemeinschaft. Man könnte vielleicht ebenso gut von einer diatomeen—chrysomonadienenartendominierten diatomeenbetonten *Fragilaria crotonensis*—*Asterionella formosa*—*Laboea* sp.—*Polyarthra maior*—Gemeinschaft sprechen.

Wie u.a. aus den O_2 -Werten hervorgeht, ist der Kuhajärvi ein oligotropher s.str. See. Gewisse Züge in der Chemie und die dominierende Stellung der *Fragilaria crotonensis* deuten aber darauf hin, dass das Wasser des Sees ein wenig eutropher ist, als man aus der ursprünglichen Umgebung schliessen könnte. In diesem Falle dürfte die Ursache entweder in der zunehmenden Besiedlung oder in einer in produktiver Hinsicht besseren Beschaffenheit der umgebenden Moräne als gemeinhin gesucht werden können.

Der Siikajärvi liegt ebenfalls innerhalb des Granitgebiets. Von den Sedimenten ist Osmaterial obwaltend. Ausserdem etwas Moräne und Torf. Kulturboden nur dem Namen nach. Keine grösse-

¹⁾ Die in diesem Aufsatz besprochenen Planktonanalysen beziehen sich auf aus 15 cm Tiefe entnommenen Wasserproben.

ren Zuflüsse. Abfluss nach dem Vihtajärvi. Die höhere Vegetation ist überaus spärlich entwickelt.

Obschon der See ziemlich seicht ist, war der Unterschied zwischen der Oberflächen- und der bodennahen Temperatur am 26.VI.1950 beträchtlich. Der O_2 -Gehalt zeigte dagegen — wahrscheinlich — keine Gefälle. Auch im übrigen war die Chemie des Wassers, das relativ hohe pH (7.5—7.6) jedoch ausgenommen, recht typisch oligotroph s.str. Woher die unerwartete Höhe des pH kommt, bleibt im Dunkeln. Es kann jedoch sein, dass sie eine Folge der in jener Zeit, vielleicht dank zufälligen exzeptionell günstigen Verhältnissen aufgetretenen, sich auch als Wasserblüte äussernden Massenentwicklung der *Cyanophyceen* gewesen ist. Dahin deutet auch der relativ niedrige CO_2 -Gehalt.

Die Seefarbe war am 20.VI.1950 grün und die Wasserfarbe 20 Pt mg/l. Im Hinblick auf unsrige Verhältnisse war die Durchsichtigkeit (Transparenz) ziemlich gross, indem die Sichttiefe etwa 6.05 m betrug. Eine schwache durch *Fragilaria crotonensis* und *Aphanizomenon flos aquae* verursachte Trübung war jedoch im Oberflächenwasser zu verspüren.

Dank dem ziemlich ruhigen Wetter hatte *Aphanizomenon* teilweise schon die Oberfläche erreicht und am Luvufer eine typische lückenlose, dem Ufer zu immer dicker werdende Wasserblüte gebildet. Mit gleichzeitiger Berücksichtigung sowohl der Einheitszahl als des Volumens war *Fragilaria crotonensis* ohne weiteres die obwaltende Phytoplanktonart. Sie war hier sogar beträchtlich zahlreicher vorhanden als im Kuhajärvi. Die nächstgrösste Rolle spielten in hier genannter Ordnung *Asterionella formosa*, *Aphanizomenon flos aquae*, *Cyclotella stelligera* und *Spondylosium planum*. Insgesamt wurden 28 Phytoplanktonarten gefunden. Mit Ausnahme einer gewissen Dominanz der *Diatomeen* waren die verschiedenen Algengruppen relativ gleichmässig vertreten.

Die Menge des Phytoplanktons betrug am 26.VI.1950 etwa 316000 Einheiten/l oder im Volumen etwa 4.4 l/m³.ha. Auch in dem Oberflächenwasser des Siikajärvi war der Volumanteil der *Diatomeen*, obschon merkbar geringer als im Kuhajärvi, ziemlich beträchtlich, aber auch die *Cyanophyceen* (dank der Wasserblüte!) machten sich relativ stark geltend. Von den notierten Zooplankterarten gehörten 4 zu den *Ciliaten*, 3 zu den *Rotatorien* und 1 zu den *Cladoceren*. Die Volksdichte war etwa 5660 Individuen/l, entsprechend etwa 3.9 l/m³.ha.

Die Planktongemeinschaft war eine mässig protococcalenartenarme — mässig desmidienartenarme *Asterionella formosa* — *Bosmina longispina* — Gemeinschaft, bzw. eine diatomeen-protococcalen-chrysomonadinenartendominierte-diatomeenbetonte *Fragilaria croto-*

nensis—*Asterionalla formosa*—*Laboea* sp.—*Polyarthra vulgaris*—Gemeinschaft. Der Protococcal—Desmidial—Quotient war 1.3.

Laut dem relativ reichlichen Vorkommen von *Fragilaria crotonensis* und *Aphanizomenon flos aquae* dürfte der Siikajärvi ein oligotropher s.str. See von mittlerer bis höherer Bonitätsstufe sein.

Der aus dem des Siikajärvi zum Vihtajärvi fliessende Bach empfängt die Abwässer der Fabrik. Um die durchgreifende Einwirkung der letzteren auf das Bachwasser zu illustrieren, mögen die Verhältnisse in dem kleinen Stauteich *Sulkulanlampi* etwas unterhalb der Mündung des Abwassergrabens erörtert werden. Der Säuregehalt der stark tongetrübten und nach Schwefel riechenden Wassers war gross, u.a. war das pH nur 1.9. Die vorherrschende Art am 20.VI.1950 war abermals *Fragilaria crotonensis*, die nächstfolgenden aber *Lepocinclis* sp., *Chlamydomonas* sp. und *Aphanizomenon flos aquae*. Betreffs der letztgenannten Art ist zu beachten, dass sie im Siikajärvi gerade am Abfluss massenhaft angehäuft war. Es wurden 13 Arten gefunden, grösstenteils *Diatomeen* und *Cyanophyceen*. Zooplankter wurden gar nicht beobachtet. Die Volksdichte des Phytoplanktons war mit Hinsicht auf die herrschenden Verhältnisse ziemlich gross: etwa 380000 Einheiten/l, entsprechend einem Volumen von etwa 5.1 l m³.ha. Von den Algengruppen dominierten dem Volumen nach die *Diatomeen*, *Eugleninen* und *Cyanophyceen*.

Aus Tab. 1b geht sehr deutlich hervor, dass der allergrösste Teil der Plankter aus dem Siikajärvi stammte. Die empfindlicheren Arten waren durch die Säuren schon vernichtet worden und andere zeigten bald grössere, bald geringere Schädigungen. Es ist auch sehr möglich, dass ein Teil der gefundenen Plankter, wie z.B. von *Aphanizomenon*, schon tot bzw. sterbend waren. Bemerkenswert ist das verhältnismässig zahlreiche Vorkommen von *Chlamydomonas* sp., *Lepocinclis* sp. und *Characiopsis* sp. Hierbei ist zu erwähnen, dass die erstgenannte Art in der unmittelbaren Nähe der Fabrik olivengrüne Überzüge auf den von Säuredämpfen gefeuchteten Wänden des in Sand ausgehobenen Leitungsgrabens bildete. Auch die fragliche *Lepocinclis*-Art scheint ein sehr niedriges pH zu vertragen oder, wie schon ihr Fehlen aus dem Vihtajärvi andeutet, sogar zu fordern.

Der *Vihtajärvi* selbst befindet sich innerhalb eines Gneisgranitgebietes. Die Sedimente bestehen dem See zunächst aus Moräne und Ton, mehr in der Peripherie ausserdem aus Sand, Osmaterial und Torf. In der relativ dichtbevölkerten Nahumgebung ist ziemlich viel Kulturboden vorhanden.

Auch dieser See schien am 27.VI.1950 thermisch geschichtet zu sein. Das Wasser war sehr elektrolytenreich. Besonders der Gehalt an freien Säuren war beträchtlich, wie auch schon das niedrige pH

(2.5—2.6) angibt. Bemerkenswert ist weiterhin der hohe Eisengehalt. Ein schwacher Schwefelgeruch des Wassers konnte beobachtet werden. Aus den Analysen geht ferner hervor, dass die Chemie des Wassers vertikal und einwenig auch horizontal variierte. Der O_2 -Verbrauch war in Bodennähe ziemlich gross. Dies äussert sich auch in der Abnahme des Nitrats und der Zunahme des Ammoniums mit der Tiefe.

Die Seefarbe war am 20.VI.1950 grün und die Wasserfarbe etwa 10 Pt mg/l. Die Sichttiefe betrug etwa 3.25 m. Das Wasser war trüblich näher dem Ufer, und besonders an dem SW-Ufer etwas opalisierend.

Der einzige Makrophyt im See ist *Phragmites communis*. Er bildet aber stellenweise, besonders dem NE-Ufer entlang, dichte und ziemlich hohe Bestände. Die ehemals reichlichen *Equisetum* und *Nymphaeaceen* sind ausgestorben. Wenigstens bis etwa 3.5 m hinab wurde der Boden überall lückenlos von *Ulothrix variabilis* bedeckt. An manchen Stellen erreichten ihre Fädenbündel die Oberfläche. Ferner waren die *Phragmites*-Stengel recht allgemein von losgerissenen *Ulothrix*-Haufen umhüllt.

Die obengenannte Trübung war verursacht durch einen kleinen Pilz aus dem Verwandtschaftskreis von *Planktomyces*, der am 20.VI. 1950 in ungeheuren Mengen besonders in der Nähe des SW-Ufers auftrat. In der Seenmitte waren darüberhinaus fast nur eine *Chlamydomonas*-Art und *Chlamydomonas*-Zysten (dieselbe Art?), diese aber mit ziemlich grosser Volksdichte, vorhanden. Etwa 3 m vom SW-Ufer war das Plankton auch ausschliesslich des Pilzes sowohl qualitativ als quantitativ merkbar reichlicher vertreten. Von den 11 Algenarten herrschte, mit gleichzeitiger Berücksichtigung der Einheitszahl und des Volumens, *Chlamydomonas* entschieden vor, aber auch *Fragilaria crotonensis*, *Asterionella formosa* und *Aphanizomenon flos aquae* spielten eine ziemlich grosse Rolle.

Die Gesamtvolksdichte des Algenplanktons betrug in der Nähe des SW-Ufers etwa 885000 Einheiten/l oder etwa 8.2 l/m³.ha. (ohne *Chlamydomonas*-Zysten etwa 218000 Einheiten/l oder etwa 5.5 l/m³.ha), aber in der Seenmitte 129000 Einheiten/l oder 0.8 l/m³.ha (ohne *Chlamydomonas*-Zysten nur etwa 29000 Einheiten/l oder etwa 0.4 l/m³.ha). Während in der Seenmitte das Volumen des Algenplanktons unter Ausschluss der *Chlamydomonas*-Zysten in erster Linie von *Ulothrichalen*, in zweiter von *Volvocalen* beherrscht wurde, dominierten in der Nähe des SW-Ufers die *Diatomeen* mit *Ulothrichalen* und *Cyanophyceen* als die folgenden.

Auch die Zooplankter schienen häufiger in der Nähe des SW-Ufers als in der Seenmitte zu sein. U.a. wurden in der letztgenannten gar

keine metazoische Plankter gefunden, während in der Ufernähe noch 1 Rotatorien- und 2 Cladoceren-Arten notiert wurden. Dank den Ciliaten war die Volksdichte relativ gross: in der Nähe des SW-Ufers etwa 40200 Einheiten/l oder etwa 21.6 l/m³.ha und in der Seenmitte etwa 9700 Einheiten/l oder etwa 3.3 l/m³.ha.

Die Planktongemeinschaft in der Mitte des Sees war eine protococcalenartenfreie—desmidienartenfreie *Chlamydomonas* sp.—, bzw. gemischttypige¹⁾—ulothrichalen—volvocalenbetonte *Chlamydomonas*—Gemeinschaft und in der Nähe des SW-Ufers eine protococcalenartenfreie—sehr desmidienartenarme *Asterionella formosa*—*Daphnia cristata*—, bzw. eine diatomeen—cyanophyceenartendominierte—diatomeenbetonte *Fragilaria crotonensis*—*Asterionella formosa*—Gemeinschaft.

Wie sind die für das Plankton günstigeren Verhältnisse in der Nähe des SW-Ufers zu erklären? Vielleicht sind dort zahlreiche Quellen vorhanden, durch deren Einwirkung lokale Verdünnungen des Elektrolytgehalts entstehen, oder vielleicht rührt sich das am stärksten verunreinigte Wasser mehr in der Seenmitte oder gar näher dem NE-Ufer. Ufer- und Bodentiere wurden gar nicht beobachtet.

Sowohl der Boden selbst als die untergetauchten Gegenstände in dem aus dem Vihtajärvi der Bucht Vihtalahti zufließenden Bach Vihtaoja waren reichlich mit *Ulothrix variabilis* bewachsen.

Die Bucht Vihtalahti liegt gleichfalls innerhalb des Gneisgranitgebiets. Von den Sedimenten obwaltet in der Nahumgebung die Moräne. Betreffs der Fernumgebung siehe oben beim Vihta- und Kuhajärvi. Das Ende der Bucht ist von ausgedehnten Äckern umgeben. Unter normalen Verhältnissen dürfte diese Bucht gewissermassen einen Mittelwert zwischen dem Siikajärvi, Kuhajärvi und Leppävesi darstellen.

Die höhere Vegetation ist im grossen ganzen schwach entwickelt: in erster Linie mehr oder minder licht wachsendes *Equisetum limosum*, stellenweise im allgemeinen kleinere Bestände von *Phragmites communis* und *Scirpus lacuster*, in wechselnden Mengen *Nymphaeaceen* und *Potamogeton*-Arten. Eine deutliche Abnahme in der Artenzahl und auch in der Volksdichte einiger Arten gegen die Mündung des Vihtaoja hin war festzustellen.

Gemäss einer etwa 300 m von der obengenannten Bachmündung entnommenen Probe war die chemische Verunreinigung noch deutlich. Der Gehalt an Kationen und Anionen ist an sich nicht

1) Der von mir in einem bald erscheinenden Aufsatz als Gemischttypus bezeichnete Typus ist dadurch gekennzeichnet, dass die Artenzahl keiner Gruppe deutlich vorherrscht.

katastrophal, es kommen Elektrolyte in eutrophen Seen oft sogar mehr vor, das pH ist aber noch sehr niedrig, nur 3.5.

Die Seefarbe war am 20.VI.1950 bräunlich gelb, die Wasserfarbe aber dessenungeachtet 20 Pt mg/l. Die Sichttiefe betrug etwa 1.65 m.

Frei herumtreibende *Ulothrix variabilis*-Bündel waren in der Nähe der Bachmündung reichlich zu finden. Ihre Zahl nahm nach aussen hin ziemlich schnell ab und an der Stelle der Probenentnahme war die Art mit blossen Auge nicht mehr zu beobachten. Dagegen waren mit dem Winde getriebene Fädenhaufen hier und da inmitten der Litoralvegetation vorhanden.

Das Phytoplankton wurde auch hier durch den oben bereits genannten Pilz entschieden beherrscht. Die Volksdichte war aber schon geringer als im Vihtajärvi. Die dominierenden Algen waren wieder *Ulothrix variabilis* und *Dinobryon bavaricum*. Es wurden 20 Algenarten gefunden, davon ein Viertel Diatomeen.

Die Volksdichte des Phytoplanktons betrug etwa 110500 Einheiten/l, entsprechend etwa 4.4 l m³.ha, d.h. sogar weniger als in der Nähe des SW-Ufers des Vihtajärvi. Der Volumanteil der Ulothrichalen war besonders gross, während die zweitwichtigsten, die Diatomeen nur etwa ein Viertel davon ausmachten.

Das Zooplankton war durch 1 Rhizopoden-, 3 Ciliaten- und 3 Rotatorien-Arten vertreten. Die Individuenmenge per 1 l belief sich auf etwa 4100, entsprechend etwa 1.0 l/m³.ha.

Die Planktongemeinschaft war eine sehr protococcalenartenarme—sehr desmidienartenarme *Ulothrix variabilis*—*Polyarthra remata*—, bzw. eine gemischttypige—ulothrichalenbetonte *Ulothrix variabilis*—*Dinobryon divergens*—*Polyarthra remata*—Gemeinschaft. Der Protoccal—Desmidial—Quotient war 2.0.

Sowohl innerhalb und ausserhalb der Makrovegetation waren etwas Bodentiere (vorwiegend Oligochaeten) vorhanden.

Wir haben gesehen, dass das Vihtajärvi-Wasser im grossen ganzen eine vernichtende Einwirkung auf die Wasserorganismen hat. Nur einige Arten mit beträchtlicher Gedeihamplitude und gewisse Spezialisten (*Ulothrix variabilis*, *Chlamydomonas* sp., in dem Sulkulanlampi ausserdem *Lepocinclis* sp. und *Characiopsis* sp.) haben sich entwickeln und bei mangelnder Konkurrenz sogar sehr reichlich vermehren können.

Tab. 1a. Das Plankton am 20.6.-50.

	Vihtajärvi SW-Ufer		Vihtajärvi		Vihtalahti 300 m von der Bach- mündung nach aussen hin	
	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³
anktomycetes K ¹⁾	2271200	1226.4	972400	525.1	625600	337.8
	2271200	1226.4	972400	525.1	625600	337.8
phanizomenon flos aquae F...	3808	82.3			272	5.9
phanocapsa elachista K					68	0.3
elosphaerium Naegelianum K	8	0.7			4	0.3
	3816	83.0			344	6.5
lamydomonas sp.	2108	12.1	2720	15.7	136	0.8
„ Zysten	66640	266.6	10064	40.3	128	0.5
	68748	278.7	12784	56.0	264	1.3
akistrodesmus falcatus v. mirabile					204	0.1
rucigenia quadrata 4-Z					68	0.1
					272	0.2
lothrix variabilis F	272	105.7	68	26.4	1156	310.7
	272	105.7	68	26.4	1156	310.7
osterium acutum v. variabile .	68	0.3				
aurastrum alternans					68	3.4
	68	0.3			68	3.4
inobryon bavaricum					1496	3.0
„ cylindricum					136	0.3
„ divergens					4284	8.6
„ sociale	408	0.8				
	408	0.8			5916	11.9
terionella formosa	1700	253.3			272	40.4
agalaria crotonensis	12648	63.2			640	3.2
elosira distans F	204	3.7				
izosolenia longiseta					612	25.3
bellaria fenestrata					612	11.0
„ flocculosa					272	4.4
	14552	320.2			2408	84.3
araciopsis sp.	612	22.0	68	2.4	272	9.8
	612	22.0	68	2.4	272	9.8

K = Kolonien, F = Fäden, 4-Z = 4-Zellgruppen, sonst Zellen

Tabel 1a.

	Vihtajärvi SW-Ufer		Vihtajärvi		Vihtalahti 300 m von der Bach- mündung nach aussen hin	
	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³
Cryptomonas sp.					68	1.6
					68	1.6
Ceratium hirundinella	26	6.2				
Peridinium inconspicuum.....					272	7.9
„ pusillum					136	2.9
	26	6.2			408	10.8
Zusammen.....	2359702	2043.3	985320	609.9	636776	778.3
Zusammen ohne Pilze	88502	816.9	12920	84.8	11176	440.5
Zusammen ohne Pilze und Chlamydomonas-Zysten	21862	550.3	2856	42.3	11048	440.0
Diffugia limnetica	68	25.2			2	0.7
	68	25.2			2	0.7
Ciliata					136	1.8
„	3740	1275.5	952	324.6	136	46.4
Epistylis sp.?	204	69.4	14	4.9		
Laboea					68	6.2
	3944	1344.9	966	329.5	340	54.4
Polyarthra remata					60	22.7
„ vulgaris					4	13.3
Synchaeta grandis					2	13.4
Trichocerca Rousseleti	2	1.4				
	2	1.4			66	49.4
Bosmina coregoni v. coregoni ..	2	331.9				
Daphnia cristata.....	2	451.8				
	4	783.7				
Zusammen.....	4018	2155.2	966	329.5	408	104.4

Tab. 1b. Plankton am 20.6.-50.

	Sulkulanlampi		Siikajärvi		Kuhajärvi	
	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³
<i>Naabaena spiroides?</i> F	4	0.7				
„ sp. F			2	0.4		
<i>Phanizomenon flos aquae</i> F ...	5032	108.7	3536	76.4	68	1.5
<i>Throococcus minutus</i>					68	0.3
<i>Coelosphaerium Naegelianum</i> ...	4	0.3			2	0.2
	5040	109.7	3538	76.8	138	2.0
<i>Chlamydomonas</i> sp.	7752	44.7				
	7752	44.7				
<i>Planckistrodesmus convolutus</i>			272	0.2		
„ <i>falcatus</i>			68	0.4	408	0.2
„ „ <i>v. mirabile</i>			68	0.3		
<i>Mediastrium Boryanum</i>			2	0.3		
„ <i>duplex</i>			2	0.2		
			412	1.4	408	0.2
<i>Chlorella</i> sp.					68	26.4
					68	26.4
<i>Chlorella phaseolus</i>			2	0.3		
<i>Chlorella planum</i>	84	1.2	748	11.0		
<i>Chlorella alternans</i>			68	3.4		
„ <i>lunatum</i>			4	0.2		
	84	1.2	822	14.9		
<i>Chlorella</i> sp.	1888	128.4				
	1888	128.4				
<i>Chlorella Chodati</i>			135	0.3		
			135	0.3		
<i>Chlorella bavaricum</i>					1428	2.9
„ <i>cylindricum</i>					68	0.1
„ <i>divergens</i>					476	1.0
„ <i>sociale</i>			26	0.1	408	0.8
„ <i>suecica</i>					136	0.1
<i>Chlorella spirale</i>					136	0.1
<i>Chlorella akrokomos</i>			408	0.9		
„ <i>reginae</i>			272	3.3		
<i>Chlorella uvella</i>			68	32.0	6	2.8
			909	36.4	2648	7.8

Tabel 1b.

	Sulkulanlampi		Siikajärvi		Kuhajärvi	
	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³	Einheiten /100 ml	Volumen mm ³ /m ³
Attheya Zachariasi	272	16.9				
Asterionella formosa	544	83.3	1088	162.1	1836	275.6
Cyclotella comta			408	4.0		
Cyclotella Kuetzingianum			340	5.5	204	3.3
„ Meneghiniana					340	7.1
„ stelligera	680	2.4	2516	8.7	1360	4.7
Fragilaria crotonensis	21100	105.5	20740	103.7	10336	51.7
Eunotia sp.	136					
Melosira distans			408	7.1	68	1.2
„ granulata			14	3.3	2	0.5
Rhizosolenia longiseta			135	5.6	408	16.9
Tabellaria fenestrata			204	3.3	204	3.7
„ flocculosa					544	9.5
	22732	208.1	25853	303.3	15302	374.2
Botryococcus Braunii					6	1.2
Characiopsis sp.	544	19.6				
	544	19.6			6	1.2
Ceratium hirundinella	8	1.9	30	7.2	16	3.8
Peridinium cinctum.					4	1.5
„ inconspicuum			68	2.0		
„ Willei			2	0.9		
	8	1.9	100	10.1	20	5.3
Zusammen	38048	513.6	31634	443.2	18590	417.1
Ciliata			204	8.2		
Laboea			136	12.5	136	12.5
Tintinnopsis lacustris			6	0.6	12	1.3
Vorticella			204	33.4	4	0.2
			550	54.7	152	14.0
Conochilus unicornis			6	17.5		
Kellicottia longispina			2	2.9	4	5.8
Polyarthra major					2	26.3
„ vulgaris			6	20.0		
			14	40.4	6	32.1
Bosmina coregoni v. longispina .			2	290.4		
„ „ v. obtusirostris					2	290.4
Daphnia cristata					12	2687.1
			2	290.4	14	2977.5
			566	385.5	172	3023.6

Tab. 2a. Die Chemie.

	Siikajärvi		Siikajärvi	Sulkulanlampi	Vihtajärvi	
					Unterer Teil	In der Mitte
Wasserstand	26.6.50	26.6.50	20.6.50	20.6.50	20.6.50	20.6.50
Tiefe der Probeentnahme in m	0.5	5.0	0.5	0.5	0.5	0.5
Temperatur °C.....	18.8	13.3				
Leitvermögen			21.8 $\times 10^{-6}$	4324 $\times 10^{-6}$	1351.2 $\times 10^{-6}$	1318.2 $\times 10^{-6}$
Nachdampfdruckstand mg/l			22.8	843.0	281.2	305.2
Nachfärbdruckstand „			12.2	167.6	115.2	118.4
MnO ₄ -Verbrauch „			18.5	52.6	13.6	12.6
HCl unlösliche Stoffe (SiO ₂ u.a.) „			4.3	301.9	63.7	65.2
„			0.4	12.6	5.2	6.5
„			0.12	5.0	6.3	6.3
„			2.0	9.2	9.0	8.2
„			0.5	3.1	3.0	3.1
„			0.5	2.5	3.5	4.5
SiO ₄ „			2.6	516.6	185.2	185.6
SiO ₂ „	9.6	10.9				
SiO ₂ „	1.3	1.3		—	—	—
H ₂ „			0.04	0.59	0.59	0.08
O ₂ „			0	Spuren	Schwache	Spuren
O ₃ „			0	25.0	113.0	113.0
Alkalinität „			0.15			
Acidität, ml/l n/10 NaOH, Methylorange				142.0	32.5	32.0
„ ml/l n/10 NaOH Phenolphthalein				157.5	56.6	42.5
CO ₂ -H	7.53	7.60		1.90		
Wasserhärte in dH°			0.41	2.00	1.96	1.87

Tab. 2b. Die Chemie.

	Vihtajärvi		Vihta- lahti	Kuha- järvi	Kuhajärvi	
Datum	27.6.50	27.6.50	20.6.50	20.6.50	27.6.50	27.6.50
Tiefe der Probenentnahme in m	0.5	9.5	0.5	0.5	0.5	10.0
Temperatur °C.....	19.3	11.6			19.6	11.0
E. Leitvermögen	1377.0 $\times 10^{-6}$	1228.0 $\times 10^{-6}$	180.1 $\times 10^{-6}$	45.0 $\times 10^{-6}$		
Abdampfrückstand mg/l	295.8	299.2	71.2	40.4		
Glührückstand „	106.6	110.2	41.6	25.2		
KMnO ₄ -Verbrauch „	9.8	15.3	40.6	17.2		
In HCl unlösliche						
Stoffe (SiO ₂ u.a.) „			5.8	5.0		
Al „			2.0	0.7		
Fe „	6.0	7.0	0.38	0.18		
Ca „			4.0	3.6		
Mg „			1.7	1.5		
Cl „	5.5	5.5	1.5	0.5		
SO ₄ „	194.8	191.9	24.2	7.4		
O ₂ „	10.2	4.8			10.1	9.8
CO ₂ „	—	—	—		3.0	3.4
NH ₃ „	0.42	1.06	0.04	0.04		
NO ₂ „	Schwache	Spuren	0	0		
NO ₃ „	102.0	56.0	11.0	0		
Alkalinität „				0.35		
Azidität, ml/l n/10 NaOH ₃						
Methylorange	29.5	29.0	2.0			
„ ml/l n/10 NOaH						
Phenolphthalein	43.0	42.5	6.0			
pH	2.54	2.56	3.50		7.24	7.30
Härte in dH°			0.93	0.85		

Some observations on the feeding of Protoza on Freshwater Algae

by

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INTRODUCTION

During 1947—48, in connection with studies on the ecology of the algal flora of slow sand filter beds of waterworks, sand- and bottom-living algae from the filter beds were kept in vessels in the laboratory. Glass microscope slides, placed on the sand in the vessels, were removed at weekly intervals and the algae upon them counted. Many algal species, which were abundant at the beginning of these experiments, rapidly decreased and in certain cases disappeared after two or three weeks. This applied particularly to unattached diatoms, while epiphytic diatoms and Chlorophyceae grew well and in time became abundant (Table 1).

Table I. *Number of Algae per sq. mm. on Slides in Culture Vessels*

	1 week	2 weeks	3 weeks	4 weeks	5 weeks	6 weeks	7 weeks	8 weeks
<i>Achnanthes minutissima</i>	10	31	54	53	68	97	130	183
<i>Amphora ovalis</i>	3	+	6	3	7	8	3	6
<i>Cocconeis placentula</i>	—	—	+	5	7	34	24	44
<i>Cymbella ventricosa</i>	2	+	—	—	—	—	—	—
<i>Navicula dicephala</i>	+	5	17	12	2	4	—	—
<i>Navicula lanceolata</i>	12	10	11	2	—	—	—	—
„ <i>pupula</i>	3	2	1	—	—	—	—	—
„ <i>radiosa</i>	4	3	+	—	—	—	—	—
„ <i>rhynchocephala</i>	40	66	18	3	2	—	—	—
<i>Nitzschia acicularis</i>	32	15	6	3	—	—	—	—
„ <i>palea</i>	7	5	—	—	—	—	—	—
„ <i>linearis</i>	95	88	70	14	9	+	—	—
„ <i>recta</i>	12	9	2	+	—	—	—	—
<i>Pinularia Brebissonii</i>	2	+	—	—	—	—	—	—
<i>Ulvella frequens</i>	+	6	8	28	36	22	28	+
<i>Chaetopeltis orbicularis</i>	—	—	—	—	6	16	40	48
<i>Phormidium molle</i>	10	30	52	29	57	61	78	69

When the cultures had been in the laboratory for a month, the contents of many frustules of the bottom-living diatoms were absent or greatly contracted, although occasional individuals of the same species appeared to be in a healthy condition. In similar experiments performed a month later protozoa with ingested diatoms in their bodies were observed on the slides. Moreover, the ingested species were those which were in course of disappearance. Since no information could be found in the literature relating to the rates at which protozoa feed on algae, it was felt that data of some value might be obtained by feeding cultures of the former with cultures of algae, and determining the rate at which the latter were consumed.

METHODS AND MATERIAL

The most abundant protozoa in the vessels were the ciliates *Uroleptus piscis*, a species of *Oxytricha*, and a species of *Chilodon*, the last being very abundant after the cultures had been in the laboratory for two months. Cultures of *Chilodon* were obtained by a dilution method, in which 2ml. samples were transferred with a wide-mouthed pipette from the sand surface of one of the vessels and mixed with 5ml. of filtered water from the same vessel. A 1ml. sample of this was added to a 100ml. flask containing 10ml. of a culture of *Nitzschia palea* (Kütz.) W. Smith. In this way several cultures containing only the ciliate *Chilodon* were obtained. The unialgal cultures used for feeding the ciliates were raised by the methods recommended by Pringsheim (1946).

Preliminary observations on the feeding of *Chilodon* on *Nitzschia palea* indicated that the latter were ingested in considerable quantity by this ciliate, certain individuals containing as many as 40 diatoms in their bodies. Various stages in the digestion of the frustules could be distinguished, the chromatophores of the ingested algae showing various degrees of contraction and ranging in appearance from that of the healthy diatom to a condition in which only two small, dark patches, at either end of the frustule were observable. At the latter stage the digestion of the contents seems to be complete, for it is in this condition that the frustules are excreted by the animal. As the feeding of the ciliates progressed, the numbers of live diatoms tended to decrease, while empty frustules accumulated. In some of the flasks, in which the initial concentration of living diatoms was low, only empty frustules remained after a few days.

The ciliates reproduced quite rapidly, their density in the flasks being estimated by means of a haemocytometer. In view of their large size and their low density in the cultures, it was however necessary

to count the number of individuals in the whole area bounded by the two transverse channels and the ends of the counting cell (i.e. in 12 cubic mm). Within the latter the ciliates were killed by withdrawing a little of the water by applying filter paper to one of the open ends, and replacing it with a few drops of 1% formalin, a makeshift method which gave fairly satisfactory results. At a concentration of 3 ciliates per 10 cubic mm the error of the counts was 40%; at a concentration of 7 the error was 23%, while counts of cultures with some 20 ciliates per 10 cub. mm had an error of only 10%. The numbers of diatoms were also estimated with the help of a haemocytometer.

The excretion of the frustules, after the cell-contents had been digested, made it possible to assess the number devoured in a given time, since the indestructibility of the frustules made it unnecessary to know the rate at which the diatoms were reproducing, — information which would have been essential had green algae been used as food. In fact, to estimate the number of diatoms eaten in a given time, it was necessary to determine only the density of the ciliates in the culture and the rate at which the digested frustules were excreted into the solution. Apart from this, however, the average number of diatoms undergoing digestion per ciliate and the density of living diatoms in the culture were also determined.

EXPERIMENTS

1. In the first successful experiment 2ml. of a culture of *Chilodon* was pipetted into each of three 100ml. flasks. To the first was added 5ml. of a healthy culture of *Navicula dicephala* (Ehr.) W. Smith with a density of 490 cells per 10 cub. mm.; to the second, 5ml. of a culture of the same diatom containing 80 cells per 10 cub. mm.; and to the third, 5ml. of culture containing 80 cells per 10 cub. mm. The final density of diatoms in the flasks was 350, 150, and 60 cells per 10 cub. mm. respectively, and the density of *Chilodon* in each was estimated at 4 per 10 cub. mm. One hour before the experiment was started, the numbers of diatoms were counted in 30 *Chilodon*-individuals taken from the original culture in which the latter were feeding on *Nitzschia palea*. This count showed that the *Chilodon* had eaten most of the diatom population, and that the average number of *Nitzschias* per ciliate was two, 56% of those examined containing no diatoms in their bodies.

Preliminary observations had indicated that the rate of ingestion of diatoms was very rapid, several being ingested within ten minutes of the addition of the ciliates to the diatom culture so that the necessity of undertaking frequent counts of the numbers of diatoms

undergoing digestion was realised. Four counts were made within the first 24 hours and two per day on the following days. The numbers of living and dead diatoms, and the numbers of ciliates in the cultures were determined only once each day.

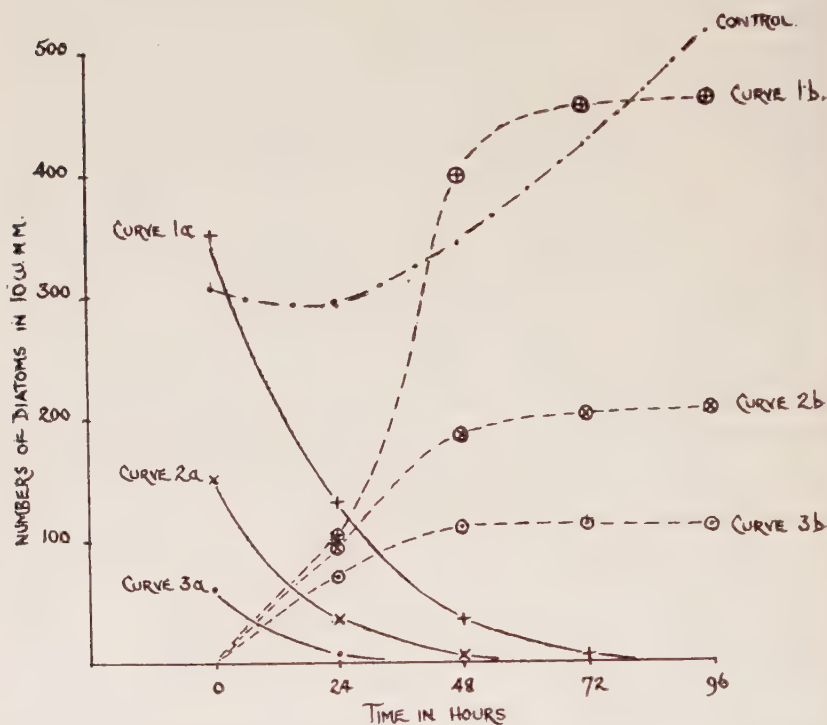


Fig. 1. Feeding experiment with *Chilodon* and *Navicula dicephala*. Graphs show numbers of living (solid lines) and dead diatoms (broken lines) in flasks with different densities of diatoms.

The curves plotted in Fig. 1 show the effect of the feeding ciliates on the diatom population; curves 1a, 2a and 3a, representing the numbers of live diatoms in the three flasks, indicate a rapid decrease as the experiment progresses. The initial decreases were not, however, entirely due to the activities of the protozoa, since the curve representing the growth of diatoms in the control flask in which no ciliates were feeding, also shows a preliminary decrease. This is due to the fact that the diatoms tend to adhere to the walls of the culture vessels and only severe shaking will dislodge them.

Curves 1b, 2b, and 3b in Fig. 1 show the rate of accumulation of the dead diatom frustules in the three flasks. From them and from the estimates of the changes in density of the ciliate populations,

plotted in Fig. 2, the rate of feeding of the latter at different stages in the experiment have been determined. During the first 24 hours period the rate of feeding in the three flasks (1, 2, 3) was approximately equal, varying between 13 and 17 diatoms per ciliate per 24 hours. Between the 24th and 48th hours the rate of feeding was limited in flasks 2 and 3 by the lack of adequate numbers of diatoms. During this period the estimated number of diatoms eaten per ciliate in flask 2 fell to 13 as against 17 during the first 24 hours, while in flask 3 the number has halved. The ciliates in flask 1 during the same period increased from 7 to 13 per 10 cub. mm., and their rate of feeding rose to 29.7 diatoms per day. Between the 48th and 72nd hours feeding had almost stopped in flask 3, and the feeding rates in flasks 1 and 2 fell to 4 and 3 diatoms per ciliate respectively. By the end of the fourth day no living diatoms were found in any of the flasks.

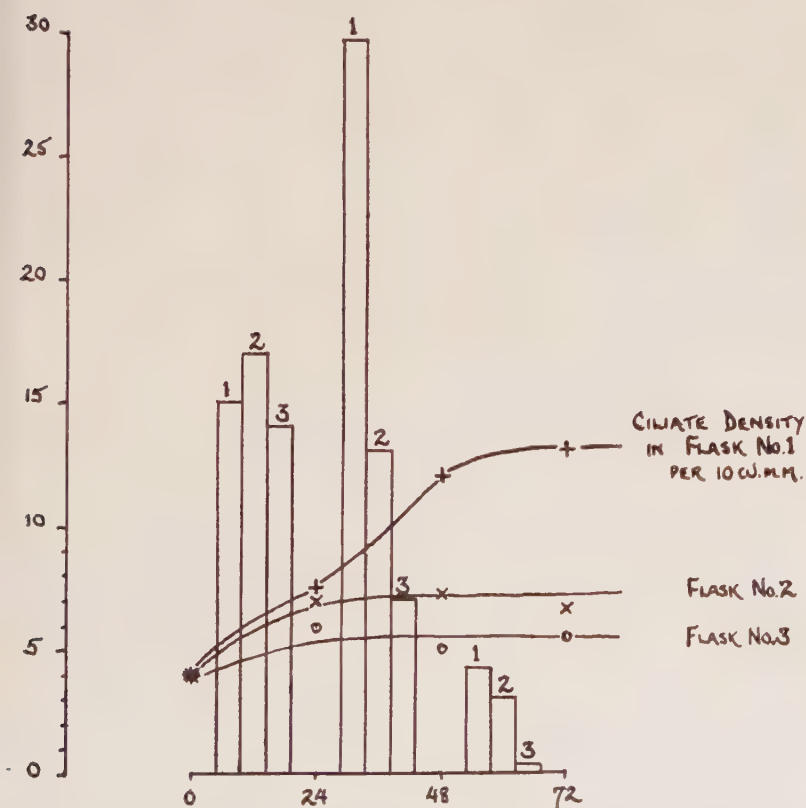


Fig. 2. Histograms showing estimated numbers of diatoms eaten per ciliate per 24 hours. Graphs showing increases in the ciliate population.

Table 2 gives the results of the counts made to determine the average numbers of diatoms found in twenty *Chilodon*-individuals at different stages of this experiment. The numbers in twenty individuals were counted for each of the three flasks, four counts being made on the first day and two on each succeeding day, 480 ciliates being examined in all. As might be expected, the numbers of diatoms ingested are directly related to the feeding rate of the *Chilodon*, being greatest and averaging 16 per individual during the period when feeding was most rapid. The largest number of diatoms ingested by any one *Chilodon* was 23.

TABLE 2.

Numbers of *Navicula dicephala* individuals ingested by *Chilodon* at different times during experiment 1.

	Flask 1.		Flask 2.		Flask 3.	
	a.	b.	a.	b.	a.	b.
3 hours	4.3	9	1.0	5	1.1	3
7 hours	7.7	20	4.0	9	4.0	8
16 hours	9.0	15	7.2	17	4.2	10
24 hours	16.0	23	8.1	17	5.3	15
29 hours	12.0	21	6.5	14	2.5	12
48 hours	2.2	9	1.7	16	0.3	1
67 hours	2.3	12	0.5	5	0	0
72 hours	0.9	5	0	1	0	0
96 hours	0.5	2	0	0	0	0

Column *a* = Average number of diatoms ingested per individual. (20 ciliates examined in each case).

Column *b* = Maximum number of diatoms found ingested.

2. In a second experiment carried out with *Chilodon* an attempt was made to determine the effects of water-movements on its feeding. Two 100ml. flasks, each containing 10 ml. of a culture of *Chilodon* (5 individuals per 10 cub. mm) feeding on *Navicula pupula* Hust. (400 individuals per 10 cub. mm.) were prepared. An air stream was bubbled through one flask so that the culture was gently agitated throughout the experiment, the rate of bubbling being approximately one bubble per second. Samples were withdrawn from the flasks at intervals of six hours, and in each 20 *Chilodon*-individuals were examined to determine the average number of diatoms ingested. The results represented in Figure 3, show a very obvious effect of the

agitation of the culture. No explanation can be offered to account for the decline in the numbers of diatoms ingested after 12 hours, since there were still adequate numbers of living diatoms available. The experiment, however, shows that water movement may exert a marked influence on the rate of feeding of the ciliate, and in nature this factor may account for quite marked differences in the size of diatom populations in still and running water.

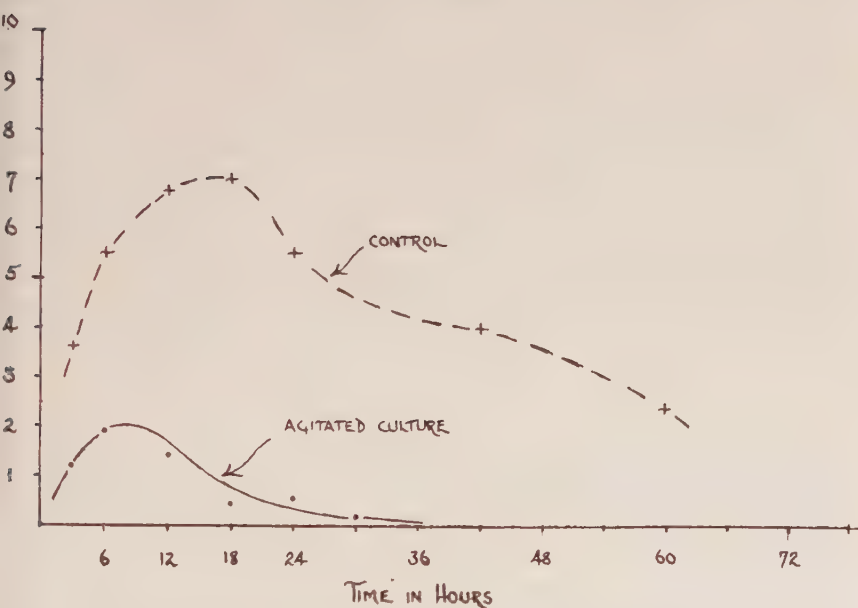


Fig. 3. Feeding of *Chilodon* on *Navicula pupula* when culture vessel was agitated. Curves show numbers of ingested diatoms per ciliate.

In some of the large culture vessels, containing sand and water from the filter beds, considerable numbers of *Uroleptus piscis* developed, and later a species of *Oxytricha*. The same dilution method, by means of which cultures of *Chilodon* had been prepared, was used to obtain cultures of both of the other ciliates which were fed initially on *Navicula pupula*.

In *Chilodon* diatoms are easily seen within the body so that it is not difficult to make direct counts of the numbers ingested. In both *Uroleptus* and *Oxytricha*, however, ingested diatoms are not seen clearly through the body wall; moreover, the far greater numbers of diatoms usually ingested, and the swift and erratic movements of these ciliates make direct counts impossible. This difficulty was overcome by adding a drop of a 1% solution of formalin to the drop of

water on the slide containing the ciliates, which not only killed them, but caused them slowly to disintegrate. Counts of the numbers of diatoms ingested could then be made with ease.

3. When a culture of *Oxytricha* feeding on *Navicula pupula* had almost devoured the diatom population, it was found that in twenty of the ciliates the average number of diatoms ingested was 5.6. Two hours after this estimate was made, 2ml. of the *Oxytricha*-culture was added to 8ml. of a healthy culture of *Navicula dicephala* in a 100ml. flask. The concentration of *Oxytricha* and of the diatom in the flask was found to be 2.3 and 650 individuals per 10 cub. mm. respectively. Throughout this experiment the numbers of living and dead diatoms in the flask were estimated every 24 hours, and the average number of diatoms in the bodies of ten of the *Oxytricha*-individuals was determined at the same time. The results of the experiment set out in Table 3, show that the maximum rate of feeding was between the 72nd and 96th hours, when 47 diatoms per ciliate were devoured. The average number of diatoms undergoing digestion was 41 per ciliate when the feeding rate was at a maximum, whilst the greatest number of *Naviculas* found in any one *Oxytricha* was 49.

TABLE 3.

Experiment 3. OXYTRICHA fed on a Culture of NAVICULA DICEPHALA. (Densities in 10 cub. mm. of culture-solution).

		Density of Live Diatoms	Density of Dead Diatoms	Density of Ciliates	Av. No. Diatoms eaten per 24 hours	Av. No. Diatoms found in Ciliate	Max. No. Diatoms found in Ciliate
Initial	Density	650	0	2.3	—	—	—
After	24 hours	470	105	2.6	43	36	42
	48 hours	310	230	3.2	45	40	45
	72 hours	190	390	3.8	46	39	49
	96 hours	143	590	4.2	49	41	46
	120 hours	60	760	4.1	40	32	39
	144 hours	17	745	5.2	3	10	15

4. While the previous experiment was in progress, a further culture of *Oxytricha* was prepared in order to study its behaviour when fed on *Nitzschia palea*. 2ml. of the *Oxytricha*-culture, which had been feeding on *Navicula pupula*, was added to 8ml. of a healthy culture of *Nitzschia palea* in a 100ml. flask; the concentration of the ciliate and of diatoms in the flask was then found to be 2.4 and 1010

individuals per 10 cub. mm. respectively. The concentrations of living and dead diatoms and of ciliates in the flask were estimated every 24 hours.

TABLE 4.

Experiment 5. *OXYTRICHA* fed on a Culture of *Nitzschia palea*.

(Densities in 10 cub. mm. of culture solution)

	Density of Live Diatoms	Density of Dead Diatoms	Density of Ciliates	Av. No. Diatoms eaten per 24 hours	Av. No. Diatoms found in Ciliate	Max. No. Diatoms found in Ciliate
Initial Density	1010	0	2.4	—	—	—
After 24 hours	1480	250	2.4	104	57	73
48 hours	1475	470	2.8	79	79	85
72 hours	1600	730	3.2	81	71	93
96 hours	1830	1150	4.4	96	66	90
120 hours	1990	1810	7.3	90	70	88

Table 4 shows that the initial concentration of diatoms was such that, although they were being devoured by the ciliate at a considerable rate, the density of living diatoms in the flask continued to increase. The ciliates themselves multiplied quite rapidly, the density increasing from 2.4 to 7.3 per 10 cub. mm. in 5 days, while their feeding rate remained fairly constant, varying between 79 and 104, with an average rate of 90 diatoms per *Oxytricha* per 24 hours. The average number of *Nitzschias* undergoing digestion within the body of an *Oxytricha* at any one time was found to be much greater than when this ciliate was fed on the larger diatom, *Navicula dicephala*, being 68.6. The greatest number of *Nitzschias* found in any one *Oxytricha* was 93.

5. In a culture of *Uroleptus piscis*, raised by the dilution method and fed on *Nitzschia palea*, the protozoan ingested the diatoms in considerable numbers, the average number counted within the body of one of the ciliates at a given time being 70. The feeding rate of this species would thus appear to be about the same as that of *Oxytricha*. Unfortunately all the feeding experiments, attempted after these preliminary observations had been made, were without success, since the ciliate died off after a short time for no apparent reason.

6. Observations on the types of algae eaten by *Chilodon*, *Oxytricha*, and *Uroleptus* in the large culture vessels, and in samples taken

directly from the filter beds, indicated that only on rare occasions were green algae ingested. It remained uncertain whether this was due to the usual low density of such algae so that there was little chance of the ciliates eating these species, or whether these protozoa were strictly diatom-feeders. Cultures of *Scenedesmus quadricauda* (Turp.) Bréb., *S. obliquus* (Turp.) Kütz. and *Pediastrum boryanum* (Turp.) Menegh. were therefore raised to determine whether such ciliates would in fact feed on green algae. *Chilodon* and *Oxytricha*, which had been fed on diatoms, were transferred to cultures of these green algae and examined at intervals of 24 hours for four days. No evidence was obtained that any of these algae was eaten. In a further series of observations the ciliates were added to mixed cultures of the green algae and *Nitzschia palea*. Here again the ciliates ingested none of the green algae, though they fed on the diatoms at a considerable rate.

FIELD OBSERVATIONS AND DISCUSSION.

For several months, prior to carrying out these feeding experiments, fortnightly examination of the algal growths on the surface of the filters and on glass slides placed in the filter beds never disclosed any protozoa, but in mid-February of 1948 large numbers of them were found on the slides amongst the filamentous growths of *Diatoma elongatum*. *Chilodon* was abundant, *Uroleptus piscis* was frequent, and many other forms were found, namely *Amoeba proteus*, *Diffugia* sp., *Cyphoderia* sp., *Actinophrys sol*, *Coleps* sp., *Oxytricha* sp., and *Stylonychia* sp.

The fact that the protozoa were found among these filamentous growths and among attached diatoms (e.g. *Gomphonema olivaceum* (Lyngb.) Kütz), and not on the bottom, where filamentous growths were scarce, is in itself of interest. In a paper on the integration of some protozoan communities, PICKEN (1937) presented evidence that freshwater protozoa occur in differentiated communities of herbivores, detritus feeders and carnivores, associated with green and blue-green algae and bacteria. He suggests that this association is determined by the mucilaginous surface of the algal filaments and of the diatoms, as well as by the mucous secretion of the protozoa, which result in the adhesion of diatoms to the filaments and the movement of the protozoa over the hydrophilic substrate provided by them.

His observations point to the conclusion that the protozoa are 'bound' to the surface of the filaments, and that it is not the presence of a food supply alone (see NOLAND 1925) which leads to the deve-

lopment of the association. Field-observations showed that rich diatom-growths on mud adjacent to patches of blue-green algae were entirely devoid of ciliates, although these were feeding on the same species of diatoms in the blue-green community. It therefore appears that the substrate (e.g. a filamentous alga) may be of great importance for the stability of the protozoan population, and that the persistence of the association depends on the properties of the substrate, rather than on the kind of food present. PICKEN's observations seem to be confirmed in the case of the protozoan community of the filter beds, since there protozoa were found only amongst filamentous growths. It should be noted, however, that in the cultures, in which filamentous algae were absent, feeding nevertheless took place at a considerable rate.

An examination of 20 individuals of *Chilodon* found amongst the attached filamentous growths on slides removed from the beds in February (see table 5), showed, by comparison to the cultures, that in most cases the ciliates had by no means eaten to capacity. The average number of ingested diatoms was about six, as compared with almost 30, when these ciliates were feeding at their maximum

TABLE 5. Diatoms eaten by *Chilodon* found among attached growths in filter beds.

(1)	1 <i>Nitzschia</i> sp. (small)	1
(2)	3 <i>Cymbella</i> , 1 <i>Achnanthes</i>	4
(3)	8 <i>Nitzschia</i> (small)	8
(4)	12 <i>Nitzschia</i> , 1 <i>Cymbella</i>	13
(5)	12 <i>Nitzschia</i> (small)	12
(6)	4 <i>Gomphonema olivaceum</i> , 2 <i>Navicula gracilis</i>	6
(7)	18 <i>Nitzschia</i> (small)	18
(8)	5 <i>Cymbella</i>	5
(9)	2 <i>Gomphonema olivaceum</i>	2
(10)	15 <i>Nitzschia</i> (small)	15
(11)	1 <i>Gomphonema</i> , 1 <i>Cymbella</i>	2
(12)	2 <i>Navicula pupula</i> , 1 <i>Cymbella</i>	3
(13)	1 <i>Pinnularia</i> , 1 <i>Nitzschia</i> (small)	2
(14)	15 <i>Nitzschia</i> (small)	15
(15)	1 <i>Gomphonema olivaceum</i> , 1 <i>Cymbella</i>	2
(16)	1 <i>Nitzschia</i> (small)	1
(17)	—	0
(18)	2 <i>Cymbella</i> , 2 <i>Gomphonema olivaceum</i>	4
(19)	7 <i>Navicula radiosa</i>	7
(20)	5 <i>Cymbella</i>	5

TOTAL = 125

Average No. of Diatoms ingested = 6.25 per *Ciliate*.

rate in the culture flasks. There are four possible explanations for the considerable discrepancy between the numbers of diatoms found in ciliates feeding 'in vitro' and the numbers found in those taken from the filters.

- (i) The rate of feeding in the filters might be limited by the density of the diatom-population.
- (ii) The ciliates in the filters might have been feeding on bacteria, as well as on diatoms (PICKEN 1937), so that their demand for algal food would not be as great as in the cultures.
- (iii) There is something inherent in the essentially artificial conditions in the culture vessels which causes a marked acceleration in the rate of feeding 'in vitro'.
- (iv) Water-movements in the filters might have been responsible for the uptake of a smaller quantity of algal food.

Later examinations of the body contents of individuals of *Chilodon* taken from the filters showed that the average number of diatoms ingested was always low. Similarly, *Oxytricha* and *Uroleptus* from the filters never contained more than half the number of diatoms which they were known to be able to ingest in culture.

Among the other protozoa that eat algae found in the filters species of *Diffugia*, *Cyphoderia* and *Arcella*, belonging to the Order Testacea were sometimes found containing a few small diatoms and occasional unicellular green algae. Of the ciliates, *Coleps* was seen with ingested unicellular green algae, a species of *Frontonia* had eaten naviculoid diatoms in small numbers, and *Stylonychia* was also observed to feed on diatoms. If one compares the size of these protozoa with those used in the feeding experiments, none of them would seem to have eaten to capacity in the filters.

Since many of these organisms are not dependent only on one source of food, but feed simultaneously on algae, bacteria and detritus (SANDON, 1932), the study of their food-requirements under natural conditions may be very complex. All that can at present be stated with certainty is that some protozoa are capable of devouring diatoms in considerable numbers, particularly when these plants are their only source of food, and it would seem that, if ciliates are numerous, they may have a marked effect on the composition of the bottom-living algal flora. This is supported by an observation on glass slides, which had been in the filters in the beginning of April 1948 for one week, on which large numbers of dead frustules of unattached diatoms, with chromatophores absent or greatly contracted, were observed. These had clearly been eaten by some animal, and since ciliates were at that time present in large numbers with ingested

diatoms amongst the filaments of *Diatoma elongatum* Ag. growing on the slides, it seems very probable that the former were responsible for the 'massacre' of these unattached diatoms.

SUMMARY

In laboratory cultures of bottom-living algae it was observed that unattached diatoms were eaten by ciliates and an attempt was therefore made to determine the rate at which these protozoa feed on algae. Cultures of certain ciliates were prepared and fed on unialgal cultures of diatoms of known concentration, with the following results: —

- 1). *Chilodon*-individuals feeding on *Navicula dicephala* can eat 30 diatoms per 24 hours. (Expt. 1).
- 2). *Oxytricha*-individuals feeding on *Navicula dicephala* can eat 47 diatoms per 24 hour (Expt. 3).
- 3). *Oxytricha*-individuals feeding on *Nitzschia palea* can eat 90 diatoms per 24 hours (Expt. 4).

In another experiment, in which one of the cultures was agitated, it appeared that water-movements may considerably reduce the rate of feeding of protozoa (Expt. 2).

Experiments in which the ciliates *Chilodon* and *Oxytricha* were added to cultures of green algae (*Scenedesmus* spp. and *Pediastrum*) indicate that these ciliates are strictly diatom-feeders (Expt. 6).

The results of the various experiments are discussed in relation to field observations.

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Personalia

Edgardo Baldi

Il 10 agosto di quest'anno si è prematuramente spento a Pallanza sul Lago Maggiore Edgardo Baldi, uno dei più noti idrobiologi italiani.

Era nato a Milano il 20 luglio 1899 e aveva compiuto i suoi studi



universitari a Pavia, allievo di Rina Monti, di cui dopo la laurea, conseguita nel 1920, fu per qualche tempo assistente e collaboratore.

In un primo tempo si era occupato di problemi della fisiologia del sistema nervoso degli Insetti, che affrontò con metodi sperimentali e con una impostazione meccanica personale. Nel 1923 passò un anno a Parigi al „Laboratoire d'évolution des êtres organisés” dedicandosi a studi di radiobiologia sotto la direzione di Caullery e di Lacassagne.

Di ritorno in Italia, dopo un intermezzo di attività giornalistica, riprese la ricerca scientifica rivolgendo la sua attenzione all'indagine

idrobiologica, di cui apprese da Rina Monti la tecnica e la passione; essa costituì da allora il principale interesse della sua vita.

Un primo contributo di ricerche idrobiologiche del Baldi è rappresentato dal lavoro sui „Copepodi Lariani” pubblicato nella monografia sul Lago di Como, diretta dalla Monti. Questa memoria segna l'inizio di una serie di lavori sui Copepodi italiani, di cui ben presto il Baldi divenne un competente specialista. In tale campo di studi egli non si limitò a indagini di pura sistematica, ma seguì quell'indirizzo di indagini sulle variazioni geografiche e sulla suddivisione della specie in unità subspecifiche, che può indicarsi con il nome di Microsistematica o di Sistematica genetica. Ebbe in tale campo il modo di indagare specie e razze di Diaptomidi di varie parti di Italia.

Conseguita nel 1925 la libera docenza in Zoologia generale e passato al seguito della Monti all'Università di Milano, il Baldi vi tenne per incarico ripetuti insegnamenti di Biologica generale, di Zoologia e di Idrobiologia. Dopo la morte della Monti resse per qualche tempo la direzione dell'Istituto di Anatomia comparata.

In questo periodo svolse un fecondo programma di indagini limnologiche sui laghi alpini e sul Trasimeno, ritornando ancora sulla meccanica della locomozione degli Artropodi e facendo alcune osservazioni sulla struttura dei cromosomi giganti della *Drosophila*.

Un importante complesso di indagini, compiute in collaborazione con G. P. Moretti, ha avuto per scopo la valutazione del materiale planctonico („carico biologico”) portato da un fiume (l'Adda) all'uscita da un lago (lago di Como).

Altro vasto programma di ricerche idrobiologiche è quello svolto dal Baldi sul lago di Tovel (Trento) (1937—40) con particolare riguardo al caratteristico fenomeno dell'arrossamento, dovuto al ciclo fisiologico di un *Glenodinium*. Questo interessante fenomeno fu indagato nel quadro di una completa visione idrobiologica del lago.

Frattanto per munifica donazione del Dott. Marco De Marchi, illuminato mecenate delle Scienze Naturali, era stato fondato a Pallanza sul Lago Maggiore l'Istituto Italiano di Idrobiologia. Di questo il Baldi fu nominato nel 1939 primo direttore. Malgrado la guerra poco dopo iniziata e le conseguenti difficoltà economiche, che resero enormemente difficile la prima sistemazione dell'Istituto e la sua successiva attività, il nuovo direttore seppe dargli subito una perfetta organizzazione materiale e scientifica. Dopo una fase di rallentata attività durante il periodo bellico, subito a guerra finita, l'Istituto di Pallanza poté rapidamente assurgere a fama, non solo italiana, ma internazionale, divenendo uno di quei punti di contatto e di riferimento che servono così efficacemente ad avvicinare gli studiosi di diversi paesi.

A questo scopo contribuì molto efficacemente l'organizzazione di alcuni convegni su problemi idrobiologici, genetici, ecologici, evolutivisti, cui parteciparono parecchi fra i più noti cultori di tali studi. Accanto al Baldi e ai suoi collaboratori, Pirocchi, Buzzati-Traverso, Tonolli, Cavalli, ecc., l'Istituto di Pallanza, attrezzato per una simpatica ospitalità scientifica, divenne frequente soggiorno preferito di numerosi scienziati italiani e stranieri. Ripetute visite del Direttore a Istituti scientifici esteri e partecipazioni a congressi contribuirono a creare intorno al centro di Pallanza una fitta rete di relazioni internazionali. L'attività svolta da Edgardo Baldi in questo campo organizzativo ha fattivamente contribuito allo sviluppo delle ricerche idrobiologiche in Italia.

Le indagini limnologiche compiute dal Baldi e dai suoi collaboratori in questo ultimo periodo sono sopra tutto caratterizzate dall'indirizzo genetico microevolutivo applicato alle popolazioni planctoniche e particolarmente al problema della loro stabilità. In tale indirizzo furono studiati i problemi dell'isolamento spaziale in seno a un bacino lacustre e della formazione di endemismi. Furono affrontati pure con brillante impostazione i problemi del trofismo lacustre, del ciclo delle lipovitamine, ecc.

Interessanti sono anche alcuni articoli di sintesi su problemi generali di Idrobiologia e di Filosofia della scienza, campo di studi che il Baldi coltivò sempre con competenza e con non comune vivacità d'ingegno.

Se anche in qualche momento la sua opera scientifica potè sembrare soverchiata da una impronta alquanto giornalistica, essa non di meno segna un efficace contributo all'indagine idrobiologica e biologica in genere, per cui sia i risultati obiettivi, che forse maggiormente la acuta impostazione dei problemi legano al nome di Edgardo Baldi un durevole ricordo. L'organizzazione dell'Istituto di Pallanza, assieme ai primi 6 volumi delle Memorie dell'Istituto, rappresenta un permanente monumento alla sua memoria.

UMBERTO D'ANCONA.

Padova, 13 novembre 1951.

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Walther Arndt

Ein Leben für die Wissenschaft

von

FERDINAND PAX

(Bremerhaven)

Mit 1 Bild

Erinnerungen sind entweder höchste Poesie, wenn sie sich auf lebendiges Glück beziehen, oder brennender Schmerz, wenn sie vernarbte Wunden berühren.

IWAN ALEKSANDROVIČ GONČAROW.

Es war in den letzten Oktobertagen des Jahres 1910. Ich hatte mich kurz vorher in Breslau habilitiert und bereitete gerade meine erste Kollegstunde vor. Da meldete sich bei mir der erste Zuhörer, ein Student der Medizin, der durch sein gepflegtes Äusseres wie seine guten Umgangsformen sofort angenehm auffiel. Es war WALTHER ARNDT. Bei diesem Besuch trat er mir gegenüber, wie ich ihn später unzählige Male gesehen habe, in einem knapp sitzenden blauen Anzug, in der Hand die schwarze Bombe, die rechte Schulter leicht vorgebeugt und um die Lippen ein verbindliches Lächeln, das seinem Antlitz etwas ungemein Liebenswertes verlieh. Er äusserte den Wunsch, die von mir angekündigte Vorlesung „Grundzüge der experimentellen Zoologie“ zu hören. Im Laufe der Unterhaltung ergab sich, dass er aus dem Riesengebirge stammte und dass unsere Väter Schulkameraden gewesen waren. Diese Unterredung zwischen dem Breslauer Privatdozenten und dem nur fünf Jahre jüngeren Zuhörer war der Anfang einer Freundschaft, die uns mehr als drei Jahrzehnte verbunden hat. Erst der Tod hat dieses Freundschaftsband zerrissen.

Fast sieben Jahre sind verflossen, seit das Leben dieses von der Natur mit mannigfachen Vorzügen bedachten Mannes ausgelöscht wurde, dessen Herz der Wissenschaft, seiner schlesischen Heimat und der geliebten Schwester gehörte. Aber noch heute ergreift die Fachgenossen, die sich ihm über den Tod hinaus verbunden fühlen, eine tiefe Erregung, wenn sie sich der Vorgänge erinnern, die seine Verurteilung herbeiführten. Der Tod unseres Freundes belastet nicht nur die Denunzianten, deren Zeugnis WALTHER ARNDT dem Volksgerichts-

hof auslieferte. Vor dem Richterstuhl des eigenen Gewissens wird sich auch jeder Fachgenosse mitschuldig bekennen müssen, der durch aktive Mitarbeit in der Partei seine Sympathie für die politischen Ziele und vor allem die Methoden des Nationalsozialismus bekundet hat, und er wird, wenn er ehrlich ist, als Milderungsgrund auch nicht das von der deutschen Zoologenschaft eingereichte Gnadengesuch gelten lassen, dessen Wirkungslosigkeit jedem Kenner der Verhältnisse von vornherein unzweifelhaft war. Die Machthaber des Dritten Reiches haben niemals einen Zweifel darüber gelassen, wie sie Defaitisten behandeln würden, deren Verbrechen darin bestand, sich in der schwülen Atmosphäre des politischen Machtrausches den klaren Blick für die Wirklichkeit bewahrt und offen die Wahrheit bekannt zu haben, ohne zu fragen, ob dieses Bekenntnis ihnen selbst nützt. Den Wenigen aber, die sich damals nicht darauf beschränkten, die auch vom Volksgerichtshof niemals angezweifelte wissenschaftlichen Verdienste des Verurteilten hervorzuheben, sondern sich zu dem Menschen ARNDT bekannten, wird es ein kleiner Trost, aber immerhin ein Trost sein, dass das Bewusstsein, in seines Lebens schwersten Stunden von seinen Freunden nicht verlassen gewesen zu sein, ihm das Sterben erleichtert hat.

Am 8. Januar 1891 wurde WALTHER ARNDT in Landeshut in Schlesien geboren als Sohn des zoologisch und botanisch stark interessierten Veterinärrates FEDOR ARNDT, in dessen Händen von 1890—1928 die Leitung des Städtischen Schlachthofes lag. Den ersten Schulunterricht empfing er in der Volksschule seiner Vaterstadt. Später besuchte er das Landeshuter Realgymnasium, das er Ostern 1909 verliess, um in Breslau Medizin und Naturwissenschaften zu studieren. An dem Realgymnasium wirkte damals als Oberschullehrer ADOLF ROTH, der nicht nur eine umfassende Kenntnis der heimischen Flora besass, sondern es vor allem verstand, die seiner Führung anvertraute Jugend für die Wissenschaft vom Leben zu begeistern. „Was aus seinem Unterricht hervorwuchs, das war das lebende Tier in seiner Mannigfaltigkeit, die lebende Pflanze, die auch zwischen den Blättern des Herbariums nicht welkte“. ARNDT hat zusammen mit seinem Freunde, dem jetzt in St. Louis tätigen Zoologen VIKTOR HAMBURGER, dem Andenken dieses trefflichen Mannes einen Nachruf gewidmet, der als Denkmal pietätvoller Gesinnung ebenso den verdienten Pädagogen wie die beiden Verfasser ehrt. Lernte der heranwachsende Knabe unter der Leitung ADOLF ROTHs die heimische Flora kennen, so weckten in ihm die Liebe zur Vogelwelt häufige Besuche der v. WALLENBERG-FENDERLINSCHEN Bibliothek, in der sich eine ansehnliche Sammlung heimischer Vögel befand. Vor allem aber war es die reizvolle Umgebung seiner Vaterstadt, die ihn zu Beobachtungen in der freien Natur

anregte. Bieten doch nur wenige Städte Schlesiens dem Naturfreunde eine ähnliche Fülle lohnender Wanderziele wie Landeshut. Schon frühzeitig galt ARNDTS besonderes Interesse der Wasserfauna seiner Heimat. LAMPERTS „Leben der Binnengewässer“ war ihm beim Studium des Landeshuter Muschelteiches ein getreuer Berater. Schon als Schüler begann er mit planmässigen Beobachtungen im Aquarium. Im Alter von 16 Jahren veröffentlichte er seinen ersten Aufsatz über die jährliche Nahrungsmenge eines Hechtes.

Im Jahre 1905 starb an seinem Geburtstag die Mutter. Umso inniger schloss er sich an seinen Vater und die fünf Jahre jüngere Schwester an. Unter des Vaters Anleitung erwarb er sich zum Teil schon während seiner Schulzeit jene umfassenden veterinärmedizinischen Kenntnisse, die später oft das Staunen seiner Fachgenossen erregten. So bezog er, vorzüglich vorbereitet für das akademische Studium, die Breslauer Hochschule. Unter der Pflege der Schwester liess er in Landeshut ausser einem Formikarium etwa 120 lebende Tiere aus allen Klassen der Vertebraten zurück mit genauen Anweisungen über wöchentlich vorzunehmende Gewichtsfeststellungen.

In Breslau wirkte damals als Zoologe und vergleichender Anatom WILLY KÜENTHAL. Die Schlesische Friedrich-Wilhelms-Universität hat wenige Hochschullehrer besessen, die sich an rednerischer Begabung, aber auch an pädagogischem Geschick mit KÜENTHAL messen konnten. Für ARNDTS Entwicklung war es von ausschlaggebender Bedeutung, dass er schon zu Beginn seiner Studienzeit in ein Institut kam, in dem Zoologen mit grosser museologischer Erfahrung wirkten. Auf diesem Gebiete hätte er in Deutschland damals nirgends bessere Lehrmeister als WILLY KÜENTHAL und CARL ZIMMER finden können. Über Entwicklungsgeschichte las in Breslau ULRICH GERHARDT. Zellenlehre und Histologie trug EMIL ROHDE vor. Ich selbst behandelte anfänglich Experimentalzoologie und Vererbungslehre. Nach dem Fortgang ZIMMERS übernahm ich die Pflege der Systematik, Ökologie und Tiergeographie. So durfte der zoologische Lehrplan in Breslau als reichhaltig gelten. ARNDT hat nicht nur sämtliche zoologischen Vorlesungen gehört, die während seiner Studienzeit in Breslau gehalten wurden. Er hat sich auch an den meisten Exkursionen beteiligt, die damals auf die akademische Jugend eine starke Anziehungskraft ausübten. Allerdings lagen die Verhältnisse in Breslau auch besonders günstig. Dr. PAUL SCHOTTLÄNDER, ein Schüler des Breslauer Botanikers FELIX ROSEN, hatte der Universität 1911 zu ihrer Hundertjahrfeier ein Kapital überreicht, dessen Zinsen ausschliesslich für Studien- und Forschungsreisen verwendet werden sollten. So standen dem Botanischen und dem Zoologischen Institut ausser kleineren Beträgen, die der Universitätskurator für Lehraus-



M. Ardh.

flüge bereit stellte, zusammen jährlich 10000 Mark zur Verfügung. Die marinen Expeditionen leitete KÜKENTHAL selbst, aus dessen Munde wir häufig den Ausspruch hörten: „Das Meer ist die hohe Schule des Zoologen“. 1911 ging ARNDT mit der ersten Lehrexpedition der Dr. PAUL SCHOTTLÄNDERSchen Jubiläumsstiftung nach Norwegen, 1913 begleitete er KÜKENTHAL mit der dritten Lehrexpedition nach Korsika. Im Jahre 1920 hat er sich dann noch einmal einer Expedition angeschlossen, die KÜKENTHALS Nachfolger, FRANZ DOFLEIN, in die Hohen Tauern unternahm. Auf diesen Fahrten erweiterte ARNDT nicht nur seine Formenkenntnis, er lernte vor allem auch gründlich die Sammel- und Konservierungsmethoden der marinen Biologie kennen, in deren Anwendung sein Lehrer KÜKENTHAL sich als Meister erwies.

Auf unseren Exkursionen war ARNDT stets einer der Fröhlichsten. Die Ausgeglichenheit seines Wesens und seine grosse Hilfsbereitschaft sicherten ihm die Zuneigung aller Fahrtgenossen. In jenen sorglosen Jugendtagen wurden die Freundschaftsbande geknüpft, die ihn mit dem heute in Coimbra tätigen Zoologen ERNST MATTHES, dem 1943 in London verstorbenen ehemaligen Direktor des Breslauer Zoologischen Gartens HANS HONIGMANN, dem Herausgeber des „Ostdeutschen Naturwerts“ HANS NEUMANN, dem Ornithologen HANS LÜTTSCHWAGER und dem 1937 verstorbenen Botaniker und Pharmakognosten ALEXANDER v. LINGELSHEIM verbanden. Aufgewachsen in der Atmosphäre des bürgerlichen Liberalismus, begegnete ARNDT im Hause seines Lehrers KÜKENTHAL den gleichen politischen Überzeugungen, und so ist er bis zu seinem Tode den demokratischen Anschauungen treu geblieben, die er sich als Student gebildet hat. In seinem Leben hat es tatsächlich keinen Zickzack gegeben, wie er es gelegentlich selbst einmal ausgedrückt hat.

Im Breslauer Zoologischen Institut lernte ARNDT zum ersten Male die Internationale der Wissenschaft kennen, und zwar trat sie ihm in einer überaus eindrucksvollen Form entgegen. KÜKENTHALS Forschungsreisen in das Nördliche Eismeer, in den Malayischen Archipel und nach Westindien, nicht zuletzt auch seine Vortragstätigkeit in den Vereinigten Staaten als Austauschprofessor hatten ihn mit Zoologen, Paläontologen und Geographen in aller Welt in Berührung gebracht. Im Auslande galt er als der beste Kenner der Wale, und sein Ansehen als Korallenforscher war unbestritten. So konnte es nicht ausbleiben, dass ihm Untersuchungsmaterial aus allen Meeren zuströmte und dass häufig Ausländer das Breslauer Institut zu Studienzwecken aufsuchten. Auf den jungen Studenten machte diese Art wissenschaftlicher Betätigung einen tiefen Eindruck.

Am Morgen des Peter und Paulstages 1914 stand ich mit WALTHER ARNDT in der Hohen Tatra auf dem Gipfel der Meeraugspitze. Wir

hatten im Frühlicht Gamsen und Murmeltiere beobachtet, an einer Felswand das bunte Gefieder eines Mauerläufers betrachtet, eine grosse Wandergesellschaft des Springschwanzes *Tetrodontophora bielanensis* beobachtet und zahlreiche Exemplare einer prächtig blauen Nachtschnecke (*Limacopsis coerulans*) gesammelt. Als wir am Nachmittag an den Csorbaer See kamen, wehten von vielen Häusern schwarze Fahnen. Die Nachricht von der Ermordung des Erzherzogs FRANZ FERDINAND hatte inzwischen auch die entlegenen Siedlungen der österreichisch-ungarischen Monarchie erreicht. Mit der lakonischen Kürze, die ihm in solchen Situationen eigen war, bemerkte ARNDT: „Das bedeutet Krieg“. Dann fuhr er in der Erörterung eines wissenschaftlichen Problems fort. ARNDTS damalige Voraussage ist eingetroffen, aber als er sie aussprach, ahnte er nicht, dass er selbst sich schon vier Monate später auf dem Wege nach Sibirien befinden würde. Nun überstürzten sich die Ereignisse. Zusammen mit einer grossen Zahl Breslauer Biologen meldete sich ARNDT in den ersten Augusttagen als Kriegsfreiwilliger. Am 18. August bestand er die medizinische Doktorprüfung, am 22. August erhielt er seine ärztliche Approbation und ging bald darauf als Feldunterarzt an die Ostfront. Am 23. Oktober geriet er in Ostpreussen mit einem Feldlazarett in russische Gefangenschaft. Einen Teil seiner Erlebnisse und Beobachtungen auf dem Wege nach Sibirien hat er in einem anschaulich geschriebenen Zeitungsartikeln geschildert, der schon im Dezember 1914 erschien. Unser Freund gehörte nicht zu den Menschen, die ein unvorhergesehenes Ereignis leicht aus der Bahn wirft und die unter dem Eindrucke eines Schicksalsschlages in dumpfer Resignation ihre Tage verbringen. Seinen unfreiwilligen Aufenthalt in Sibirien benutzte er zur gründlichen Erlernung der russischen Sprache, studierte aufmerksam Land und Leute und machte Beobachtungen über die jagdlichen Verhältnisse. Im Sommer 1915 lag in seinen Händen die ärztliche Betreuung deutscher Kriegsgefangener, die beim Bau der Atschinsk-Minusinsker Eisenbahn beschäftigt wurden. Dabei lernte er das berühmte naturwissenschaftliche Museum in Minussinsk kennen. Seine zoologischen Neigungen teilte der als Molluskenforscher bekannte Zwickauer Arzt KURT BÜTTNER, mit dem er zusammen einen Teil der Gefangenschaft, 1915/16 in Spastkoje und 1916/17 in Chaborowsk verbrachte. Nach 2½ Jahren wurde ARNDT als Arzt ausgetauscht. In die Heimat zurückgekehrt, erstattete er 1917 einen Bericht an das Preussische Kriegsministerium über die Lage in den sibirischen Gefangenenlagern, der, frei von Chauvinismus, in seiner ruhigen Sachlichkeit ein getreues Spiegelbild der vornehmen Denkart seines Verfassers ist. Anfang Mai 1918 ging er wiederum nach Russland, dieses Mal als Mitglied der Russland-Kriegsgefangenen-

Fürsorgekommission des Kriegsministeriums. Er trat diese Reise an in der festen Überzeugung, dass die Kommission von den Russen festgesetzt werden würde. Für diesen Fall hatte er sich mit wissenschaftlicher Literatur und einfachem zoologischem Sammelgerät versehen. Seine Voraussicht erwies sich als durchaus begründet. Er geriet in russische Gefangenschaft. Erst im August 1919 kehrte er über Wladiwostok, Japan, die Philippinen, San Francisco, New York und Schweden in die Heimat zurück. Eindrücke von dieser Reise hat er in seinem Aufsatz „Im Stillen Ozean“ festgehalten, der im August 1919 in der „Schlesischen Zeitung“ veröffentlicht wurde. Der zweimalige Aufenthalt in Russland hat nicht nur ARNDTS wissenschaftlichen Gesichtskreis erweitert.

Im Juni 1919 wurde er zum Dr. med., im Juni 1920 zum Dr. phil. promoviert. In den Jahren 1920 und 1921 war er als Volontärassistent am Zoologischen Institut und Museum der Universität Breslau tätig. Im April 1921 folgte er seinem Lehrer KÜKENTHAL nach Berlin. Dort übernahm er die Verwaltung der Schwämme, Würmer, Moostiere und Stachelhäuter des Zoologischen Museums, zunächst als Assistent, von 1925—1931 als Kustos, seit dieser Zeit bis zu seinem Tode als Kustos und Professor.

Seine Tätigkeit in Berlin wurde häufig durch Reisen ans Meer unterbrochen. 1923 beteiligte er sich an hydrographischen Untersuchungen, die das Marine-Vermessungsschiff „Panther“ in der Nordsee ausführte. Im Frühjahr 1926 hatte ARNDT einen Arbeitsplatz in der Zoologischen Station in Neapel. Die Tage, die ich dort mit ihm verlebte, werden stets zu den beglückendsten Erinnerungen meines Lebens gehören.

Die Pflichten eines Museumsbeamten nahm ARNDT ausserordentlich ernst. Mustergültig baute er die Poriferen-Abteilung aus; die einzig dastehende Nutzwamm-Sammlung des Berliner Museums ist sein Werk. Besonderen Fleiss verwendete er ferner auf die Vervollständigung der Poriferen-Bibliothek, für die er alle ihr fehlenden Schriften photokopieren liess. Schliesslich legte er eine Sammlung bildlicher Darstellungen von Schwämmen sowie eine sehr beachtliche Sammlung von Bildnissen solcher Zoologen an, die sich erfolgreich auf dem Gebiete der Spongiologie betätigt haben. Aber auch andere Museen erfreuten sich seiner Fürsorge. Sie galt besonders dem Breslauer Zoologischen Museum, und „the rich collections of sponges in the British Museum“ — schreibt BURTON — „have been enlarged to an appreciable extent by Dr. ARNDT's friendly actions.“

Trotz ARNDTS aufopfernder Hingabe an die Ausgestaltung des Berliner Museums trat in ihm doch der Verwaltungsbeamte zurück hinter dem Forscher, der nicht in der Aufstapelung von Tier-

material, sondern in dessen wissenschaftlicher Auswertung die wichtigste Aufgabe eines Kustos erblickte. Wie er schon als Student in Breslau dafür Sorge getragen hat, dass das Material der SCHOTTLÄNDER-Expeditionen bearbeitet wurde, so ist es auch lediglich seiner Tatkraft zu verdanken, wenn die von ROEMER und SCHAUDINN begründete „Fauna Arctica“, die einen Überblick über die nördlich des Polarkreises bekannt gewordenen 8000 Metazoen-Arten bietet, 1933 abgeschlossen werden konnte.

Nirgends haben sich seine organisatorische Begabung, sein Sinn für systematische Ordnung, die zwingende Logik seiner Gedankengänge, seine Vorliebe für statistische Formulierung wissenschaftlicher Ergebnisse, aber auch sein unzweifelhaftes diplomatisches Geschick so bewährt wie in der redaktionellen Arbeit. Einer der wertvollsten Mitarbeiter meiner „Wirbeltierfauna von Schlesien“ war WALTHER ARNDT, und als ich 1926 den Plan fasste, die „Rohstoffe des Tierreichs“ in einem grossen zusammenfassenden Werke zur Darstellung zu bringen, stand es für mich von vornherein fest, dass als Mitherausgeber nur er in Frage kommen könnte. Schliesslich wollen wir nicht vergessen, dass der 6. Band der von OPPENHEIMER und PINCUSSEN herausgegebenen „Tabulae Biologicae“, der das Zahlenmaterial aus dem Gebiete der Zoologie enthält, im wesentlichen das Ergebnis seiner selbstlosen Mitarbeit darstellt.

Sehr bemerkenswert war seine Tätigkeit als wissenschaftlicher Sachverständiger. Seine Gutachten zeugten nicht nur von einer erstaunlichen Beherrschung des Stoffes, sondern vor allem auch von einem vorbildlichen Verantwortungsbewusstsein. Oft enthielten sie neue für die Rechtsprechung wertvolle Begriffsbestimmungen.

An der Arbeit der wissenschaftlichen Vereine hat ARNDT seit jeher regen Anteil genommen. Schon während seiner Breslauer Assistentenzeit gehörte er zu den anregendsten Rednern in den Sitzungen des Vereins für schlesische Insektenkunde. In Berlin galt sein Interesse besonders der Gesellschaft für Höhlen- und Karstforschung sowie der Gesellschaft naturforschender Freunde, in der er 1935 den Vorsitz führte. Zahlreiche seiner wissenschaftlichen Arbeiten sind in den Veröffentlichungen dieser beiden Gesellschaften erschienen. Aber auch in den Sitzungen der Deutschen Ornithologischen Gesellschaft und der Deutschen Entomologischen Gesellschaft war er ein gern gesehener Gast. Mit besonderer Freude nahm er an dem von A. WILLER geleiteten Fischereiwissenschaftlichen Kolloquium teil, das in der Reichsanstalt für Fischerei in Friedrichshagen abgehalten wurde. Trotz seines enzyklopädischen Wissens war er von grösster Bescheidenheit. Diese Eigenschaften machten ihn überall zum beliebten Debattenredner. In dem Bund deutscher naturwissenschaftlicher Museen, in dessen Vorstand

er von 1929—1936 wertvolle Arbeit leistete, hat ARNDT von Anfang an eine erhebliche Rolle gespielt. Auch der Internationalen Vereinigung für theoretische und angewandte Limnologie gehörte er seit ihrer Gründung (1922) an. Fast regelmässig hat er an den Jahresversammlungen der Deutschen zoologischen Gesellschaft teilgenommen, wie er auch die Internationalen Zoologenkongresse in Budapest (1927), Padua (1930) und Lissabon (1935) besucht hat.

Das Ausland hat ARNDTS wissenschaftliche Bedeutung frühzeitig erkannt. 1929 ernannte ihn die Peking Society of Natural History zu ihrem korrespondierenden Mitglied, 1932 die Bulgarische Naturforschende Gesellschaft zu ihrem Ehrenmitglied. Seit 1938 gehörte er der Internationalen Zoologischen Nomenklatur-Kommission an. In dem gleichen Jahre verlieh ihm der König der Belgier eine mit seinem Bild geschmückte Plakette „en souvenir et en reconnaissance de la part contributive que vous avez apportée à l'étude des collections scientifiques réunies par le Roi au cours de son voyage en Extrême-Orient, en 1928—29“, wie es in dem Begleitschreiben des Chefs des Königlichen Kabinetts hiess.

Allen Aufgaben der *V o l k s b i l d u n g* brachte ARNDT ein warmherziges Interesse entgegen. So übernahm er nicht nur gern volkstümliche Vorträge, sondern schrieb auch häufig Aufsätze für die Tagespresse. Ausserordentlich umfangreich war seine publizistische Tätigkeit. Das fast 250 Nummern umfassende Verzeichnis seiner Schriften überrascht vor allem durch die Vielseitigkeit seiner wissenschaftlichen Interessen. Mit Vorliebe behandelte er, besonders in den letzten beiden Jahrzehnten seines Lebens, Probleme der *M u s e u m s k u n d e*. Seine auf jahrelangen Versuchen und Beobachtungen beruhenden Ausführungen über Alkoholfragen im Naturkunde-Museum sind von grosser praktischer Bedeutung. So beschäftigte er sich mit der Frage nach der Ersetzbarkeit des reinen durch vergällten Äthylalkohol, prüfte den Verdunstungsschwund des Alkohols in Spirituspräparaten, die Veränderungen des Wassergehaltes und des pH-Wertes des Präparatenalkohols, vor allem aber den Verschluss der Alkoholpräparate. Der von ihm geführte Nachweis, dass durch Zusatz von 5% Glycerin zum Konservierungsalkohol der Verdunstungsschwund bis auf die Hälfte, durch Auftragen von Vaseline auf die Schliffstreifen der eingeschliffenen Glasstopfen auf 1/300 herabgesetzt werden kann, gestattet es fortan allen zoologischen Museen, sehr erhebliche Ersparnisse an Geld und Arbeitsstunden zu machen. Das von ARNDT zusammen mit O. THIEL und C. ZIMMER herausgegebene „Spezialisten-Verzeichnis“ wurde sehr bald zu einem unentbehrlichen Hilfsmittel der Faunistik. Grosse Verdienste erwarb sich ARNDT um die Förderung und zweckmässige Ausgestaltung der zoologischen *Bibliographie*. Machten seine

museologischen Literaturberichte uns mit Neuerscheinungen bekannt, die vorher bibliographisch noch gar nicht oder nur sehr lückenhaft erfasst worden waren, so gab seine Zusammenstellung der Bibliographien der faunistischen Gesamtliteratur der deutschen Landesteile zum ersten Male einen befriedigenden Überblick über die Leistungen auf einem anderen bisher wenig beachteten Gebiet der Bücherkunde. Seine Literaturberichte über die rezente Höhlenfauna wurden auch ausserhalb des engen Kreises der zoologischen Fachgenossen viel benützt. Einen durch Vollständigkeit und Zuverlässigkeit seiner Angaben vorbildlichen Führer durch das kaum noch übersehbare Gebiet der Schwammliteratur stellt seine gross angelegte „Bibliographia spongiologica“ dar, von der 1940 die erste Lieferung erschien. Angesichts der wirtschaftlichen Verhältnisse ist leider zu befürchten, dass dieses Werk ein Torso bleiben wird.

ARNDT'S Beschäftigung mit bibliographischen Fragen brachte ihn in enge Berührung mit der Geschichte der angewandten Zoologie. Bei seiner grossen Literaturkenntnis konnte es nicht ausbleiben, dass er immer wieder, besonders beim Studium des ältesten Schrifttums, auf Angaben stiess, die der Aufmerksamkeit früherer Forscher entgangen waren oder die eine neue Deutung nahelegten. So entstand sein Hinweis auf die bereits im Talmud erwähnte Verwendung von Mehlwürmern als Vivarienfutter und sein Aufsatz über bildliche Darstellungen von Schwämmen im kretisch-mykenischen Kulturbereich, in dem er die Verwendung von Badeschwämmen durch den Menschen zurückverfolgen konnte bis in das zweite Bronzezeitalter und die Zeit der ersten kretischen Hegemonie (1900—1750 v. Chr.).

Die Reihe seiner medizinischen Veröffentlichungen wurde durch seine Doktordissertation eröffnet, die er unter KÜSTNER'S Leitung im Laboratorium der Universitäts-Frauenklinik in Breslau ausarbeitete. Sie beschäftigte sich mit dem physiologischen und pathologischen Vorkommen morphologisch darstellbarer Lipoide in den Geschlechtsorganen des Weibes. Nur einmal hat er später noch ein rein medizinisches Thema behandelt, nämlich das Krankheitswesen und die Gesundheitspflege seines Heimatkreises Landeshut. Alle übrigen Arbeiten betreffen Grenzgebiete zwischen Zoologie und Medizin, so seine kritischen Sammelreferate über die Rolle der Insekten und Vögel im Arzneischatz der alten Völker, sein Bericht über die in naturwissenschaftlichen Museen auftretenden Berufskrankheiten, seine Untersuchungen über natürliche und künstliche Badeschwämme in hygienischer Beziehung und sein interessanter Beitrag über Spongien und Polychäten als Gesundheitsschädlinge, vor allem aber seine beiden grossen 1940 erschienen Monographien der zoogenen Riechstoffe und der als Heil-

mittel gebrauchten Rohstoffe des Tierreichs. Diese meisterhaften, von einer souveränen Beherrschung der medizinischen und der zoologischen Literatur zeugenden Darstellungen allein würden genügen, dem Namen ARNDT für immer einen ehrenvollen Platz im wissenschaftlichen Schrifttum zu sichern.

Seine schriftstellerische Tätigkeit auf veterinärmedizinischem Gebiet ist wenig umfangreich. Sie beschränkt sich auf die Mitteilung gelegentlicher Beobachtungen über Sperlinge als Fleischschädlinge und das Auftreten von Simuliasis in Schlesien.

Sehr frühzeitig setzte seine physiologische Arbeit ein. Sie begann mit einer sorgfältigen Untersuchung über das Vorkommen von Fett bei Aktinien. Über die Cholesterinfettsäureester-Verdauung bei Aktinien, Trikladen und Hirudineen hat er 1922 auf der Jahresversammlung der Deutschen Zoologischen Gesellschaft in Würzburg berichtet. ARNDT war der erste, der das Auftreten leuchtender Tausendfüsse in Schlesien feststellte. Zusammen mit P. MANTEUFEL behandelte er die Turbellarien als Träger von Giften. In dem gleichen Jahre (1925), in dem diese Arbeit erschien, hielt er in der Jahresversammlung der Deutschen Zoologischen Gesellschaft in Jena einen Vortrag über die toxischen Eigenschaften der Trikladen. Die Reihe dieser Untersuchungen wurde abgeschlossen durch einen Aufsatz über Polykladen und marine Trikladen als Giftträger, der kurz nach seinem Tode erschien. Noch ungedruckt sind einige Beiträge über den Integumentwechsel der Poriferen, Rotatorien, Kinorhynchen, Hirudineen und Pentastomiden, die in den „Tabulae Biologicae“ veröffentlicht werden sollen.

Ausserordentlich reizvoll sind ARNDTS ökologische Untersuchungen. Er hat als erster in den Sudeten planmässig speläobiologische Beobachtungen angestellt und damit eine sichere Grundlage für alle späteren Forschungen geschaffen. Zugleich verdanken wir ihm die erste zusammenfassende Darstellung der Tierbevölkerung der Meereshöhlen. Die Frucht eines Ferienaufenthaltes in Landeshut ist die kleine Studie über die Bedeutung der Klebgürtel der Pechnelken für die Kleintierwelt, in der er nachwies, dass 73% der Opfer der Klebgürtel Zufallsgäste darstellen. Sehr eingehend hat sich ARNDT mit den biologischen Beziehungen zwischen Schwämmen und Krebsen beschäftigt. Dieser Arbeit folgte eine gemeinsam mit F. PAX ausgeführte Untersuchung über das Zusammenleben von Krustenanemonen und Schwämmen, in welcher der Anteil der Poriferen am Aufbau des Fremdkörperskeletts des spongiobionten *Parazoanthus axinellae* klargestellt und die Vergesellschaftung als Epökie gedeutet wurde. In der gemeinsam mit K. VIETS vorgenommenen Analyse der biologischen Beziehungen zwischen Spongien und Arachnoideen wurde das Verhältnis zwischen *Unio-*

nicola crassipes und Spongilliden als Parasitismus erkannt. In weiteren Kreisen bekannt geworden ist ARNDTS Name durch seine Statistik der in Deutschland nachgewiesenen Tierarten. Erst durch diese entscheidungsvolle Arbeit wurde der Nachweis erbracht, dass in Deutschland rund 40000 Spezies vorkommen, von denen 33000 auf die Landtiere, 7000 auf die Bewohner der Binnengewässer entfallen. Ihnen stehen 4000 Meerestiere gegenüber. Höhlen und Grundwasser beherbergen etwa 750, die Salzstellen des Binnenlandes 1100 Arten. 10000 Spezies, also ein Viertel der gesamten Tierbevölkerung leben parasitisch. 6700 Arten der deutschen Fauna sind mikroskopisch, werden nicht grösser als 1 mm. Etwa 4⁰/₁₀ aller bisher bekannten Tierarten kommen in Deutschland vor.

ARNDTS Hauptbedeutung liegt auf dem Gebiete der zoologischen Systematik, und hier war es in erster Linie das Studium der Poriferen, insbesondere der Süsswasserschwämme, durch das er sich bleibende Verdienste erworben hat. Fast die Hälfte seiner wissenschaftlichen Arbeiten ist dieser Tiergruppe gewidmet. Seine Bearbeitungen der Spongien in DAHLS „Tierwelt Deutschlands“, den „Tabulae Biologicae“ und der „Tierwelt der Nord- und Ostsee“ von GRIMPE und WAGLER dürfen als Muster systematischer Monographien gelten, wie auch seine Untersuchung über das Vorkommen geographischer Rassen bei marinen Schwämmen den erfahrenen, kenntnisreichen Forscher verrät. Seine Entdeckung einer neuen mit einem hohen Mass von Wahrscheinlichkeit als Tertiärrelikt zu deutenden Poriferengattung (*Ochridaspongia*) im Ochridasee hat mit Recht lebhaftes Interesse erregt. Neben den Schwämmen waren es die Turbellarien, vor allem die Bachtrikladen, denen ARNDTS besondere Aufmerksamkeit galt. Die deutschen Landplanarien-Funde verzeichnete er mit grösster Sorgfalt. Dass er aber auch mit der Systematik anderer Tiergruppen wohl vertraut war, beweist seine mit dem Norweger GRIEG durchgeführte Bearbeitung der arktischen Brachiopoden sowie seine Publikation über die Copeognathen der Arktis.

ARNDTS wissenschaftliche Bedeutung als Faunist und Tiergeograph ist unbestritten. Sein Anteil an der hydrobiologischen Erforschung Bulgariens ist schon von berufener Seite eingehend gewürdigt worden. Mühevolle, durch Jahre hindurch fortgesetzte Untersuchungen über die Verbreitung des Alpenstrudelwurms veranlassten ihn, sich eingehend mit dem Begriff des Eiszeitrelikts zu beschäftigen. Gemeinsam mit dem bulgarischen Zoologen BURESCH veröffentlichte er eine Abhandlung über die Glazialrelikte Bulgariens und Mazedoniens. Wertvolle Belehrung dürfen wir aber von einer noch ungedruckten Arbeit über die Zoogeographie der Nord- und Ostsee erwarten, die sich auf eine Prüfung ihrer Schwammfauna stützt.

So sehr sich ARNDT mit seiner ganzen Persönlichkeit für die Organisation internationaler wissenschaftlicher Bestrebungen einsetzte, so vermochte er sich zeitlebens doch nicht dem Zauber des Bodens zu entwinden, auf dem seine Wiege stand. Seiner Arbeit liebster Teil galt seiner schlesischen Heimat. Das zweibändige, von KUNICK herausgegebene Heimatbuch des Kreises Landeshut verdankt der Tatkraft und der Opferbereitschaft WALTHER ARNDTS seine Entstehung, und die Abschnitte des Buches, die er selbst verfasst hat, gehören zu dem Besten, was von zoologischer Seite über das schlesische Gebirge geschrieben worden ist. Nach seiner Verurteilung kreisten seine Gedanken immer wieder um diesen Teil seines Lebenswerkes. In einem Brief, den er Ende Mai 1944 aus dem Gefängnis an seine Schwester richtete, traf er Bestimmungen über die faunistischen Aufzeichnungen, die er in Landeshut sichergestellt hatte und die nach seinem Tode Eigentum des dortigen Heimatmuseums werden sollten. Über ARNDTS Vaterstadt weht heute der polnische Adler, und trotz grosszügiger Unterstützung durch die an der Breslauer Universität tätigen polnischen Gelehrten war es mir bisher nicht möglich festzustellen, ob dieses wissenschaftliche Vermächtnis ARNDTS gerettet worden ist.

ARNDTS Veröffentlichungen auf dem Gebiete des Naturschutzes sind ausschliesslich seiner engeren Heimat gewidmet.

Wer das Lebenswerk unseres Freundes kritisch mustert, dem fällt sofort auf, dass seine literarische Produktion zwar in einem ungewöhnlich jugendlichen Alter einsetzt, dass sie aber erst nach Erreichung des 35. Lebensjahres ihre volle Reife erreicht. Die Mehrzahl seiner wertvollsten Arbeiten ist sogar erst nach seinem 45. Lebensjahre erschienen. Zum Teil beruht dies natürlich darauf, dass fünf Jahre seines Lebens durch Kriegsdienst und Gefangenschaft seiner Forscherarbeit verloren gegangen sind. Als deutsche Denunzianten ihn dem Henker auslieferten, stand er auf der Höhe seines wissenschaftlichen Schaffens. Zwei Schwammgattungen (*Arndtanchora* und *Waltherarndtia*), eine Mallophagengattung (*Arndtiella*), ferner 12 Arten und 2 Varietäten aus den Stämmen der Urtiere, Schwämme, Würmer und Gliedertiere sowie eine Pilzart tragen ARNDTS Namen.

Immer geneigt, die Leistungen anderer neidlos anzuerkennen und menschliche Schwächen zu entschuldigen, war ARNDT gegen sich selbst von unbestechlicher Sicherheit des Urteils und vorbildlicher Objektivität, und so würde er selbst kein Verständnis dafür aufbringen, wenn wir hier ein Bild seiner Persönlichkeit entwerfen würden, das nicht der Wirklichkeit entspricht. WALTHER ARNDT war auf seinem Spezialgebiete eine anerkannte Autorität, deren Hilfe nicht nur die deutschen Fachgenossen gern in Anspruch nahmen, ein Mann von erstaunlicher Literaturkenntnis, dem sich nur wenige

Zoologen in dieser Hinsicht vergleichen konnten, ein erfolgreicher Organisator auf dem Gebiete der Museumskunde und der Bibliographie. Mit vollem Rechte hat v. Lengerken den Verstorbenen als einen Gelehrten gekennzeichnet, der „sich mit höchstem Idealismus seinen wissenschaftlichen Aufgaben unter völligem Einsatz seiner Person gewidmet“ hat. Wie er während eines schweren Fliegerangriffs auf Berlin unter Lebensgefahr Brände im Zoologischen Museum löschte, so hat auch sonst die Rücksicht auf das eigene Wohl niemals seine Haltung beeinflusst. Als er zum Kustos des Berliner Zoologischen Museums ernannt werden sollte, liess er freiwillig einem jungen Kollegen den Vortritt, weil dieser verheiratet war und Kinder hatte.

Ehrfurcht vor der Vergangenheit erfüllte ARNDTS Wesen. Mit erstaunlicher Sicherheit las ein erfahrener Graphologe aus ARNDTS Schriftzügen menschlichen Takt und grosse Güte sowie eine ungewöhnliche Zartheit der Empfindung heraus. Und BURTON äussert sich in seinem in der „Nature“ veröffentlichten Nachruf folgendermassen: „My impression was of a kindly and courteous scholar, who spared no pains to be of the greatest assistance to a colleague“. Er gehörte zu den glücklichen Menschen, denen die Arbeit niemals eine Last war.

1928 trat ARNDTS Vater in den Ruhestand und siedelte nach Berlin über, wo bis zu seinem Tode im Jahre 1943 zwischen ihm und seinen Söhnen eine harmonische Lebens- und Arbeitsgemeinschaft bestand, wie sie nur wenigen Menschen beschieden ist. Der Vater wurde nun der treueste Mitarbeiter des Sohnes. Mit nie ermattendem Eifer widmete er sich den langwierigen Vorarbeiten für die „Rohstoffe des Tierreichs“ und die Statistik der deutschen Tierarten und excerpierte, unermüdlich schaffend, ganze Serien von Zeitschriften. Ein für den Privatgebrauch des Sohnes bestimmter zweibändiger Katalog der Gattungen und Arten der Cornacuspongiden ist die Frucht seines Fleisses. Dass sich in einem Hause, dem die Frau fehlte, kein gesellschaftliches Leben entwickeln konnte, ist selbstverständlich. So traf sich ARNDT mit seinen Freunden, dem Ornithologen HEINROTH, dem später nach Südamerika ausgewanderten Tardigradenforscher MARCUS und dem Säugetierspezialisten POHLE in deren Arbeitsstätten oder bei wissenschaftlichen Veranstaltungen. Seine Ferien verwendete er meist zu Studienreisen, zum Besuch von Kongressen oder zum Abschluss wissenschaftlicher Beobachtungsreihen. Die Arbeit an den „Rohstoffen des Tierreichs“ wurde fast niemals unterbrochen. Seine karg bemessene Freizeit füllte das Studium philosophischer Werke oder die Lektüre schöngestiger Bücher aus.

Mit mehreren Zoologinnen verband ihn Freundschaft — aber nicht mehr. Manches Mädchen, das seinen Lebensweg kreuzte, hat seine

Zurückhaltung wohl bedauert, und mit Recht. Denn ARNDTS ausgesprochener Familiensinn, seine Bedürfnislosigkeit und seine vornehme Gesinnung hätten die beste Gewähr für eine glückliche Ehe geboten.

Einmal im Jahre ruhte auch im Hause ARNDT die wissenschaftliche Arbeit. Das war in der Weihnachtswoche, wenn Schwester und Schwager nach Berlin zu Besuch kamen oder Vater und Sohn nach Schleswig fuhren, um Weihnachten zu feiern und das neue Jahr zu beginnen. Ein Band inniger Liebe schlang sich um diese vier Menschen so dass der greise Senior der Familie wenige Stunden vor seinem Tode im Gefühl tiefster Befriedigung sagen konnte: „Das ist das Schöne bei uns Vieren, dass einer immer für den Anderen da ist“.

In einer Zeit tiefsten moralischen Verfalls hat er bewiesen, dass es unter den deutschen Gelehrten nicht nur würdelose Lakaien und auf ihren persönlichen Vorteil bedachte Konjunkturritter gibt.

Als „Mensch der furchtlosen Aufrichtigkeit“¹⁾ machte er aus seiner pessimistischen Beurteilung der Lage niemals einen Hehl und äusserte sich in defaitistischem Sinne auch zu Charakteren, denen gegenüber grössere Vorsicht am Platze gewesen wäre. Nach einem der schweren Bombenangriffe im Herbst 1943, sprach er die prophetischen Worte: „Jetzt ist es zu Ende mit dem Dritten Reich. Es handelt sich nur noch um die Bestrafung der Schuldigen“. Eine Jugendfreundin seiner Schwester, ihr Mann und ein Berliner Zoologe erstatteten gegen ihn Anzeige²⁾. So nahm das Schicksal seinen Lauf.

Nichts kennzeichnet den Tiefstand nationalsozialistischer Rechtsprechung besser als das Urteil des Volksgerichtshofes vom 11. Mai 1944, das ARNDT für ehrlos erklärte. Das Urteil der Nachwelt lautet freilich wesentlich anders. Am 26. Juni, dem Geburtstage seiner Schwester, wurde in Brandenburg das Todesurteil vollzogen, das der Wissenschaft einen Systematiker von internationalem Ansehen, unserem Volke nach dem Ausspruche HJALMAR BROCHS, „einen der feinsten Vertreter der alten deutschen Kultur“ und seiner schlesischen Heimat einen ihrer treuesten Söhne raubte. Ich verlor meinen besten Freund.

¹⁾ So nannte MAKSIM GORKIJ den russischen Symboliker ALEXANDER BLOK.

²⁾ Erst nach mehr als 5 Jahren konnten die Verbrecher zur Rechenschaft gezogen werden: Am 22. September 1949 verurteilte das Schwurgericht Moabit Frau HANNELIESE MEHLHAUSEN zu 15, den praktischen Arzt Dr. med. SIEGFRIED MEHLHAUSEN zu 12 und den Berliner Zoologen Dr. phil. WOLFGANG STICHEL zu 8 Jahren Zuchthaus.

Verzeichnis der Veröffentlichungen Walther Arndts (1907—1948)

(Besonders wichtige Publikationen sind durch ein * kenntlich gemacht)

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A study on the metamorphosis of several species of *Atrichopogon*; two of those species could not be reared, the other six are described as new under the names of *A. speculiger*, *dubius*, *cornutus*, *alveolatus*, *hexastichus* and *polydactylus*. However, there is some doubt about the species first named being really distinct. A detailed description of the morphology and the ethology of the species is given; the descriptions concern the larvae as well as the pupae; a phylogenetical tree is constructed based on the data given. Taxonomy of the group is discussed which is very difficult owing to great individual variation, also to the fact that sometimes imagines are identical. A valuable contribution to the knowledge of that very difficult group which still is far from being satisfactorily known.

HADZI, J., Studien über Folliculiniden, Acad. Sci. et Art. Slovenica, Inst. Biol. 4/2, Ljubljana 1951, (in comm. Dr. W. Junk, publishers, The Hague) 390 p., 57 fig.

Studies on Folliculinids. — Here is a very detailed work on the Folliculinids (Bottle-animalcules), containing the description of all the known forms, arranged in several groups following the details of the shell structure; not less than 15 new genera and 23 new species are described in that first (special) part of the book. The second or general part contains several distinct chapters, dealing respectively with: (1) structure of Folliculinids with relation to their biology; (2) their life-cycle; (3) observations on cytology; (4) the so-called neck-redoubling; (5) a new parasite of Protozoans; (6) a new systematic arrangement of Folliculinids. As it can be seen from the above, this book contains an unusual amount of information; the tentative new taxonomic arrangement of the group and the very numerous new genera and species described make it necessary for specialists and indeed for all protistologists to acquire this excellent monograph.

OYE, P. VAN - Recherches sur les Rotateurs de Belgique, VI. Rotateurs d'un petit étang à Beernem, *Ann. Soc. R. Zool. Belgique*, 81, 1951, 165—177. Research on the Rotifers of Belgium, VI. Rotifers of a small pond at Beernem. Contains: Introduction. - Ecological data of the samples. - List of species. - Data concerning the species collected. - General conclusions, with remarks on the distribution of some species. The following species are new for the Belgian fauna: *Diurella brachyura* (GOSSE), *Lecane methoria* HARRING & MYERS, *Squatinella cirrata* (O. F. MÜLLER).

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The great laws of hydrobiology. A comprehensive account of the

principal laws that rule life in water. These laws are of three kinds: physical that are well known in general, but as yet insufficiently worked out by hydrobiologists; chemical, still largely unknown; and biological, especially biogeographical, that are now being studied. The writer gives the following definition of hydrobiology: A science studying the laws ruling life in water, biological associations, succession and geographical repartition of organisms.

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A general account of the present state of the study on biocenoses, and especially microbiocenoses, which are placed by the lecturer as an intermediate between phytosociology and zoosociology; microsociology has its own standing and its own methods.

GRONTVED, J. - Phytoplankton studies, 2. A new biological type within the genus *Chaetoceros*, *Chaetoceros sessilis* sp. nov., *Biol. Medd.* 18, no 17, 1951, 10 p., 7 fig., 1 pl.

Detailed description of the new species *Chaetoceros sessilis*, collected at the bottom in the North Sea. It differs from its congeners by being attached by bristles to a floating or deposited substratum.

HENDEY, N., I. — I. Littoral Diatoms of Chichester Harbour with special reference to fouling. *J. R. Microsc. Soc.* (London) 1951, Ser. III, Vol. LXXI, p. 1—86, 18 Pl.

Le Royal Naval Service est intéressé à l'étude des enduits qui encrassent les coques de navires et objets des constructions baignées par l'eau de mer. Pour parer à la formation de ces enduits, on utilise des peintures „antifouling”, généralement à base de cuivre. Hendey a institué des expériences pendant plusieurs années, en plongeant sous la surface de la mer, dans le port de Chichester (Sussex), des plaques d'acier doux couvertes de peintures contre l'encrassement. L'examen périodique, mensuel des plaques montre la façon dont elles se colonisent.

Les premiers colonisateurs sont diverses Bactéries. Leur action tend à modifier le pH des couleurs protectrices; ensuite s'installent des Diatomées. Suivant leur résistance au cuivre, elles se développent plus ou moins, certaines avec une abondance parfois exubérante. Ce sont spécialement des espèces à mucus ou pédicellées qui donnent des colonies denses, parmi lesquelles on signale *Amphora coffeaeformis*, var. *pusilla*, des *Navicula*, des *Amphora*, de petites *Amphiprora*, *Achnantes longipes*, des frondes muqueuses de *Navicula Grevillei*. Les deux dernières espèces ont permis une intéressante étude de la variation des frustules suivant leur longueur, leur largeur et leur grandeur superficielle.

Le milieu marin littoral est riche en éléments nutritifs et ne subit pas les influences dues au manque périodique de nitrates et phosphates, bien connu pour les Diatomées planctoniques. Il diffère aussi des eaux douces et de la vie terrestre étudiée par quelques auteurs dans leur action sur la variation cellulaire des Diatomées. Chez *Achnantes longipes* il y a une forme longue et une courte, déterminée vraisemblablement par l'influence du protoplaste, hypothèse à confirmer par des cultures. Ces constatations ont une réelle importance pour la taxonomie.

Des tableaux donnent l'apparition et la disparition, l'abondance de toutes

les Diatomées étudiées pour chaque mois de l'année. Certaines d'entr'elles sont saumâtres, d'autres pélophiles.

Un paragraphe est consacré à la préparation des frustules. Avant la description systématique (accompagnée de belles et nombreuses photographies) Hendey donne un aperçu de la classification qu'il a suivie dans son mémoire des „Discovery Reports” de 1932 et qui comprend, pour les *Bacillariales*, les sous-ordres suivants: 1. *Discineae*, 2. *Aulacodiscineae*, 3. *Auliscineae*, 4. *Biddulphineae*, 5. *Soleniineae*, 6. *Araphidineae*, 7. *Raphidioidineae*, 8. *Monoraphidineae*, 9. *Biraphidineae*, 10. *Surirellineae*. 144 Diatomées sont décrites et beaucoup d'entr'elles sont figurées avec synonymie, description, dimensions et notes utiles pour les spécialistes. Une abondante bibliographie complète ce travail qui peut avantageusement être consulté par ceux qui étudient la flore diatomique de la Manche et de ses environs.

H. K.

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